

# FORM AND FUNCTION IN ANGIOSPERM POLLEN<sup>1</sup>

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## ABSTRACT

In pollen morphology, as for other characters, the relation between origin, form, and function is basic for taxonomic interpretation. Physicochemical limitations to form development, structures inherited from gymnosperm ancestors, and newly evolved structures are reviewed from this point of view for a few selected angiosperm pollen types. The divergence of structures in closely related taxa suggests that pollen characters may evolve quite independently from other characters and are determined by a highly complex set of factors related to survival during transport and germination. For size and spinosity correlation with flower characters and pollination type is apparent in some cases. Special attention is given to harmomegathic functioning of the pollen grain as a whole, evidence for transfer of function is presented, and two new evolutionary trends are recognized. Peristasy involves reduction of colpate ectoapertures with retention of endoapertures, sphericity, and an exine structure distributing harmomegathic stresses equally over the surface. Latistasy results in a latitudinally oriented harmomegathic stress pattern and has been achieved in different ways. The independent origin of such trends in unrelated taxa is stressed.

In evaluating the significance of pollen characters, be it for taxonomic purposes or for interpretation of the fossil record, it is essential to consider the pollen grain as a functional unit. In the early days of pollen morphology, culminating in Wodehouse's classic *Pollen Grains*, which was published in 1935, exine morphology was generally studied in relation to intine development and behavior of the wall during changes in humidity of the environment and germination. With the introduction of acetolysis by Erdtman in 1934, attention became focussed more on the sporopollenin skeleton, revealed in intricate detail by removal of cytoplasm, intine, and outer fatty substances. The wealth of information which this method produced was first summarized in the monumental *Pollen Morphology and Plant Taxonomy* by Erdtman in 1952. While the introduction of scanning electron microscopy led to an even greater emphasis on the intricate details of exine architecture, transmission electron microscopy, especially when applied to ontogeny, provided a new impetus to the study of the entire grain. Moreover, a renewed interest in the physiology of the living grain (Heslop-Harrison, 1971a, 1971b, 1976) has stimulated an integrated study of all characters, which should ultimately lead to a pollen ecology.

When the present contribution, nevertheless, appears to concentrate mainly on the exine, this is because it incorporates a large number of taxonomically important characters which can be easily studied from herbarium specimens and also because, perforce, fossil pollen studies are entirely based on the exine skeleton. Its main purpose is to provide on this base a survey of certain widespread morphological phenomena, to consider their possible functional significance and thus to contribute to a better understanding both of their taxonomic significance and their value for interpreting the fossil record.

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## EXINE STRATIFICATION

As is well known, the angiosperm pollen wall generally consists of a cellulosic intine and a sporopollenin containing exine. Although the proportion between these two basic layers may vary, it is only in certain hydrogamous plants such as *Zostera* that the exine is totally absent. This indicates a protective function for the exine against adverse atmospheric conditions.

The exine in its complete development consists of an inner endexine and an outer ectexine. Both layers can be distinguished by stain differentiation as first demonstrated with LM by Faegri (1956) and later confirmed with TEM by Larson et al. (1962). In some cases the endexine may be absent (Palmae, Thanikaimoni, 1970), while in others it frequently is thickened near the apertures.

The endexine generally has a more uniform structure than the ectexine but may show lamellations near the aperture or, as Van Campo (1978) has recently emphasized, interior sculpture. Its ultrastructure is basically lamellated, but this may be masked by sporopollenin deposition later (Heslop-Harrison, 1971b: 88).

The ectexine shows more variation in structure, ranging from virtually homogeneous in *Degeneria* (Dahl & Rowley, 1965), granular as in *Piptostigma* (Van Campo & Lugardon, 1973), or columellate with or without an inner sole and outer tectum as in many angiosperms. The sole (formerly called foot-layer, cf. Cerceau-Larrival et al., 1975) may be homogeneous or laminated, while the tectum may bear various types of sculptural elements such as warts or spines. Frequently columellae and tectal elements combine to form complicated structures.

Two main questions arise regarding this radial differentiation in the exine:

1. What is the phylogeny of the different layers?
2. What is their function?

Before we can attempt to answer these questions a short review of exine ontogeny is necessary. In the case of the columellar exine, sporopollenin accumulates on lamellae of unit-membrane dimensions within the primexine, and, very early in the ontogeny, radially oriented probacula develop, which subsequently expand at their tops to form the tectum and at their bases to form a sole. The endexine develops later (Heslop-Harrison, 1971b).

In the case of the granular exine, it is not yet clear whether a different system operates, but the fact that transitional structures are known, such as described in Annonaceae by Le Thomas & Lugardon (1976), suggests that the difference may not be fundamental and that columellae may in fact be composed of linearly fused granules, the linear orientation being supplied by radially oriented lamellae.

However, the situation in *Polyceratocarpus* (Annonaceae) described by Le Thomas & Lugardon (1976) in which the exine essentially consists of a granular mass with a loose accumulation of larger granules on the inner side, becoming more fine grained and compacted outward, suggests a system of indeterminate growth by apposition of material from the inside. This is, of course, very different from the precisely controlled development of a typically columellar exine.

Doyle et al. (1975) have shown that granular exines occur both in gymnosperms and angiosperms, but that columellar exines are at present only known from angiosperms, although Klaus (1977) has recently described columellar structure below the alveolar zone of the ectexine in *Pinus*. However, the extinct

gymnospermous pollen type *Classopollis* has a structure which is very similar to a columellar one (Pettit & Chaloner, 1964), and recently Cornet has discovered Triassic pollen grains of as yet uncertain affinities with a very distinct reticulate-columellate exine structure (Cornet, 1977; Doyle, 1978). This suggests that a columellar organization of sporopollenin may have evolved independently in different plant groups and may not be an exclusive character of the angiosperms.

The alveolar exine type characterizing many gymnosperms is not known from recent angiosperms, although transitions may have existed in the past between the radially oriented structural elements of the middle exine layer of cycads or saccate conifers and the columellae layer of angiosperms. This possibility is suggested by the occurrence of *Clavatipollenites*-like grains in the middle Jurassic of Sweden (Tralau, 1968).

The endexine, as first pointed out by Doyle et al. (1975), is more uniformly present and laminated in gymnosperms than in angiosperms, and these authors propose an hypothesis involving reduction and subsequent reelaboration of the endexine during the transition between the two groups. As pointed out before, the basic structure of the young endexine in angiosperms is lamellate, and this would be evidence for homology, although certainly the elaboration of endexine characters, especially near the endoapertures, in this group is unmatched in gymnosperms.

A new element in angiosperm exines is the sole, which does not appear to be present in any gymnosperm pollen grain. Interestingly, this layer is either homogeneous or laminated as in certain Annonaceae (e.g., *Isolona*: "couche basale feuilletée lamellaire," Le Thomas & Lugardon, 1976) and Dipterocarpaceae (e.g., *Vatica*; laminated basal layer, Maury et al., 1975). It may be noted that in both cases this laminated layer belongs to the ectexine and is equivalent to the sole, and, moreover, that it represents, no doubt, a derived condition. Again, this demonstrates how comparatively easily in unrelated plant groups the basic process of sporepollenin deposition can be modified in any layer of the exine.

Undoubtedly such changes occur in response to selective pressure, and this brings us to the question of functional significance. Basically, any exine structure is a compromise between the protective, the harmomegathic, and the reservoir function. The protective function is evident in closed, sealing layers such as a homogeneous sole or a closed tectum. The harmomegathic function, which is the ability to absorb bending stresses such as occur during desiccation, as Wodehouse (1935) was the first to point out convincingly, has resulted in structures which prevent rupture of the exine. The reservoir function may be connected with characteristic cavities which are so widespread in the pollen of many angiosperm families, and which hold tapetum-derived materials (tryphine) that play a significant role in producing an adhesive surface ("pollenkitt") or as recognition substances. In fact, Heslop-Harrison (1976) considers the columellate layer to be the culmination of an adaptive trend for favoring outbreeding by conveyance of sporophytic recognition substances.

Since the cavities found in many gymnosperm pollen grains do not appear to carry such substances (Heslop-Harrison, 1976), it may be that their origin is related to structural strength. The tubular-alveolar structure in cycads enforces a certain rigidity, at least in the extraapertural regions, while the columellar an-

giosperm exine is probably relatively more flexible, especially the open reticulate-columellar structure. It is also of interest that the laminated endexine of gymnosperms appears more flexible than the ectexine. In this view the columellate-tectate angiosperm exine may represent also a culmination of a trend towards a more equalized distribution of bending stresses over its entire thickness. As discussed by Muller (1969) and Bolick (1978), the radially oriented columellae would serve as elements absorbing compressive forces, while the tectum would form a tensile element. The function of the endexine has at the same time become more closely related to the apertures.

Of interest in this context is the granular exine. Structurally it behaves quite differently to bending stresses, and it does not appear to have a well-developed reservoir function. Also, its potential for combining with tectate structures into the complex exine architecture such as occur in many highly evolved angiosperm pollen types, as for example in Compositae, appears limited.

This may explain the prevalence of granular type exines in many wind pollinated "amentiferous" taxa such as *Juglans* (Van Campo & Lugardon, 1973), *Ulmus*, *Alnus* and *Betula* (Nilsson et al., 1977). Here the granular infratectal structure is correlated with a rather uniformly thin exine, a lack of tryphine causing a dry surface, and an absence of any sculptural development of the tectum except small spinules. Again, it is obvious that a similar structure has evolved in close response to similar ecological requirements, i.e., wind pollination in not closely related taxa, probably in late Cretaceous time during evolution from the Normapolles complex (cf. Doyle, 1978).

In contrast to this is the situation in *Vigna* and *Phaseolus*, recently described by Stainier & Horvat (1978). These two leguminous genera which have a very similar flower morphology and presumably also pollination, differ in their exine structure. In *Vigna* a granular infratectal structure is present, and correlated with simple porate apertures, while *Phaseolus* pollen is characterized by a columellar structure and complex colporate apertures. This difference is here closely correlated with taxonomy, although its functional significance is obscure.

#### APERTURES

The local modifications of the exine structure generally termed apertures have early drawn the attention of pollen morphologists, and by now it is clear that in angiosperms a large range, from simple to complex apertures, often integrated with intinal differentiation occurs. Functionally, apertures act as regulatory harmomegathic structures, as contact points for the exchange of intine-bound recognition substances and, finally, as exits for the pollen tube (Heslop-Harrison, 1976).

Wodehouse (1935) was the first to point out that the earliest angiosperms had inherited the distal fold or sulcus from their gymnosperm ancestors, and that a large part of the morphologic variability of angiosperm apertures is related to the elimination of the distal aperture and its replacement by equatorial or peri-dispersed apertures. It appears probable that this change was related to selection for increased efficiency in pollen-stigma interaction, but it obviously also involved a complete reconstruction of the harmomegathic stress system. A first problem

to be discussed is whether the distal sulcus is strictly homologous with equatorially oriented, folded ectoapertures or colpi.

In general, spindle orientation, cleavage pattern, and polarization in the early tetrad stage appear to determine aperture location (Huynh, 1976). In the case of distal apertures, polarization is the dominant influence, as shown by Heslop-Harrison (1971a) for *Lilium*, where undivided mother cells do not develop an aperture. In Gramineae Christensen & Horner (1974) have demonstrated that influences outside the mother cells determine the location of the single aperture which is therefore not distal in the strict sense (Faegri, 1978; Huynh, 1975).

For the equatorially tricolpate pollen type it has long been recognized that apertures are initiated at specific points in the developing tetrad in such a way that they are arranged in a paired position according to Fischer's law. Here the location of the apertures is thus determined not only by polarization but also by intracellular equal spacing and intercellular positioning, resulting in a paired arrangement. The equal spacing has been shown by Tammes (1930) to represent a least surface configuration. The paired position results according to Wodehouse (1935) from phragmoplast connections for which he presents a convincing picture of an abnormally developed *Cichorium* tetrad. However, recent ultrastructural studies have failed to show evidence for the existence of such connections due to very early development of a callose wall separating the tetrad cells. Moreover, it was already pointed out by Wodehouse (1935) that, in the abnormal case of a square *Cichorium* tetrad, two apertures formed by pit connections, while opposite these two, more apertures developed at points of the cell surface not in contact with the other surfaces.

It is also instructive in this connection to observe tetrads of stephanocolpate pollen grains such as occur in *Utricularia punctata* (Thanikaimoni, 1966). Here all colpi are positioned in equally spaced paired positions. This suggests strongly that aperture induction is coordinated for the tetrad as a whole before callose deposition on the phragmoplasts takes place, and that number of apertures and their equatorial location is genetically determined, while their equal spacing is the result of physicochemical forces acting over the entire surface of the sporocyte and resulting in a least surface configuration.

At the ultrastructural level, microtubules appear to be involved in this process, and the first visible indication of future aperture sites is a plate of endoplasmic reticulum attached to the plasmalemma. Rowley (1976) considers the process of aperture formation as essentially similar in such diverse taxa as *Silene* (Caryophyllaceae), *Beta* (Chenopodiaceae), *Saintpaulia* (Gesneriaceae), *Parkinsonia* (Leguminosae), *Helleborus* (Ranunculaceae), *Citrus* (Rutaceae), and *Capsicum* (Solanaceae), while in *Epilobium* (Onagraceae) and *Tradescantia* (Commelinaceae) different processes appear to be involved. Also, Dickison (1976) stresses the fact that taxa may differ in this respect.

The change from equatorially arranged apertures to peri-dispersed ones, either colpate or porate, reflects loss of polarization and a take-over of aperture induction by forces leading to least surface configuration entirely. An interesting transitional case is the spiralization of apertures described for *Sidalcea* by Van Campo (1976) and in abnormally developed gigas pollen for *Utricularia* by Casper & Manitz (1975).

It is probable, though not yet proven by observation, that in the peri-dispersed arrangement positioning of apertures takes place for each microspore independently of its sisters in the tetrad. In this connection Waterkeyn & Bienfait's (1970) observations on *Ipomoea* pollen are of interest. These authors showed that here the callosic wall shows a thickness pattern directly related to the apertural configuration and assume that this callose template is primary. Earlier, Waterkeyn (1964) had already suggested that callose thickness differences reflect the orientation of the microspores in the tetrads and thus determine the distal pole and the position of the aperture. Willemse (1971) has described a similar phenomenon in *Pinus*, where callose formation is blocked at places where vesicles derived from the endoplasmic reticulum extrude, producing a template for the coming exine pattern. Also, Ford (1971) established for *Styphelia* that ectexine patterning is bound to the presence of callose. The hypothesis that callose functions in some way as a passive intermediate stage, transferring the transient cytoplasmic pattern as a stable template for subsequent primexine replication, therefore, seems an attractive one.

In this view, the peri-dispersed aperture configuration could result from no more than a slight difference in timing of the relevant processes, in such a way that initiation of apertures is delayed to a stage when the callose walls separating the young microspores have effectively severed polar gradients which were present before in the tetrad as a whole. As a consequence, the young microspores will tend to remain spherical, and forces leading to a least surface configuration of apertures will take over and cause a peri-dispersed distribution. It is clear that genetically this may be caused by minor mutations, and that this may easily happen in an identical way in quite unrelated taxa, which is, in fact, what is found in any survey of the taxonomic distribution of this character. This hypothesis could also form the basis for the successiform series first recognized by Van Campo (1967).

In this connection it may be pointed out that, according to Schwanitz (1953), polyploids which are often characterized by larger pollen grains with peri-dispersed apertures, have a lowered metabolism. This may have contributed to the postulated slight shift in timing of the various stages involved in the critical early phase of exine ontogeny. It may be added that extraapertural exine structure is rarely, if ever, affected.

The positioning of a large number of peri-dispersed pores, as in *Ipomoea*, differs in some respects from the configurations of peri-dispersed colpi. Tammes (1930) first showed that in the latter case the configurations found correspond to regular endospherical polyhedra. Wodehouse (1935) further elaborated on this and supposed that isotasithynic (= equilateral) stresses could produce a trischistoclastic pattern and that heterotasithynic (=unequal) stresses would lead to tetracolpate or loxocolpate configurations. His suggestion (Wodehouse, 1935: 185) that furrow configurations are the result of mechanical stresses now appears unlikely in view of the very early initiation of apertures, at a stage when the young microspores are still enclosed within the confines of the insulating callose wall of the meiocyte. Instead, the mathematical derivation by Tammes (1930) of the regular peri-dispersed aperture configurations from the point systems on a sphere appears sufficient explanation, provided colpi are equivalent to pores. He

has shown that for any given ratio between  $p$ , the radius of the touching circles,  $R$ , the radius of the sphere and the actual number of apertures preferred arrangements result, which for the lower numbers correspond to one of the five possible endospherical polyhedra. A further elaboration of this theory has been given by Fejes To'th (1964:226–237). In this view, which is close to that adopted by Van Campo (1976), the only “force” needed is the one causing equal spacing of initiation sites.

An extreme example of the operation of this principle is found in Malpighiaceae, where Lobreau (1967) could describe the various apertural configurations in strict crystallographic terminology. These variations appear here to be correlated with intergeneric differences.

Van Campo (1976) discussed the taxonomic distribution of her successiform series and showed that both taxonomic correlation (Centrospermae!) and independent origin in unrelated taxa is found.

The preceding discussion mainly referred to what may be termed primary apertures present in the ectexine, or ectoapertures. However, the endexine may develop secondarily endoapertures, either in combination or separately from the ectoapertures, indicating independent initiation, probably again made possible by a slight difference in ontogenetic timing.

In the normal case of a tricolporate grain, the endoapertures occupy the central equatorial position of each ectoaperture, but already in the heterocolpate grains the number of endoapertures is half that of the ectoapertures, although their position has not changed. In *Pardoglossum tubiflorum* (Boraginaceae) compound pores alternate with simple colpi (Clarke et al., 1979). The pores consist of a distinct circular endoaperture, covered with a finely verrucate membrane which can be interpreted as a reduced ectoaperture. The ectocolpi are of the normal narrow, invaginating type. It would be interesting to study the behavior of this pollen type during changes in humidity and while germinating.

A most intriguing case of displacement has been described by Clarke (1977) for *Lappula squarrosa* (Boraginaceae) where the plane in which the endoapertures are situated is oblique to the equatorial plane. Similar phenomena are known from Malpighiaceae and, as an abnormality, in *Lepisanthes* (Sapindaceae).

This emphasizes the different character of both types of apertures. While the ectoaperture is basically elongate (colpate) and only secondarily porate, the endoaperture located in the endexine is basically isodiametric and only secondarily elongate. The tricolporate aperture, which is phylogenetically younger than the tricolpate one, may thus represent the juxtaposition of an “inherited” colpus and a newly developed pore structure, and a large part of the diversity in higher dicotyledonous pollen types may reflect attempts to reconcile these phylogenetically, as well as functionally, different elements structurally. In a study of the pollen of *Plagiopteron* (Plagiopteraceae) Baas et al. (1979) have discussed this problem.

It is significant in this connection that the earliest tricolpate pollen types from the lower Cretaceous show no trace of endoapertures. The earliest manifestation is a slight bridging or constriction of the colpus membrane, the “geniculus” of Potonié (cf. Stanley & Kremp, 1959). This development has the important structural consequence that the infolding of each colpus is restricted to two areas

poleward of the equatorial constriction of each furrow, effectively diminishing the total volume accommodation possible. In a later stage the endoapertures become more clearly outlined in the endexine, which is soon followed by a situation in which endexinal thickenings or costae surround the endoaperture. These costae may be annular, present on the polar sides only, or restricted to the corners between equatorially elongated endoapertures and the superposed colpate ectoapertures. Also, the colpi themselves may develop costate thickenings along their margins. In general these appear to represent different solutions to the problem of combination of a fixed point structure within a folding structure. In the more extreme cases, the pore is converted into a protruding structure, taking over part of the harmomegathic functioning of the colpi which may finally disappear altogether. In other cases the endoapertures become equatorially extended and, ultimately, fused to form a ringlike structure which is frequently bordered on the polar sides by endexinal costae. This case, which will be discussed more in detail later, occurs in certain pollen types found in Lentibulariaceae, Polygalaceae, and Rhizophoraceae. Here the harmomegathic functioning is transferred from the colpi (meridional folding structures) to the endoapertures (equatorial folding structure). Other specializations are the H-shaped structures in Cornaceae, described by Ferguson (1977) and the endoapertural folds or "replis" of Celastraceae studied by Lobreau-Callen & Lugardon (1973).

It is clear that many of these developments are of considerable taxonomic significance since they seem to be restricted to a part of the higher dicotyledons. In Caryophyllales and Papaverales endoapertures are very rarely developed. In Ranunculaceae also they appear to be absent, but in other families assigned to Ranunculales they may be more frequent (e.g., Lardizabalaceae, Menispermaceae). In Trochodendrales they are weakly developed as in Platanaceae (Hamamelidales) and Eucommiaceae (Eucommiales). In Fagales the genus *Quercus* still represents all transitions between colpate-colporoidate-colporate, while *Fagus* has truly tricolporate pollen. Didymelaceae are remarkable in having two well-developed endoapertures per colpus and resemble in this respect the Albian genus *Hexaporotricolpites*.

In contrast, the subclasses Dilleniidae, Rosidae (with the exception of the order Proteales), and Asteridae have basically colporate apertures, although secondary modifications may have caused loss of endoapertures (Dipterocarpoideae) or loss of colpate ectoapertures, either leading to "pororate" types, in which the ectoapertures have become porate, or to cryptoporate types, in which any trace of ectoapertures has been eliminated and a uniform sculpture covers the endoapertures. This last phenomenon will be discussed more in detail later.

#### EXINE ARCHITECTURE

In this chapter those features of the extra-apertural exine which form what is commonly called structure and sculpture will be discussed. Since these two terms are often hard to separate, especially in the more complexly built exines, Walker & Doyle's (1975) suggestion to use the term architecture is followed here. Structure will be used as a term denoting a specific type of architectural element. Basically three different structural types can be distinguished:



- A. Columella-derived structures, mostly with a reticulate architecture.
- B. Tectal structures, mostly spinose or verrucose suprategal structures.
- C. Combined structures such as are found in the spinose exines of Compositae.

The fossil record indicates that an evolutionary progression  $A \rightarrow B \rightarrow C$  has taken place. The factors determining this have no doubt been very diverse. Transport, reservoir, and protective requirements must have been intricately interwoven, while the structures found in large grains must also have been adapted to growth during development. This makes it necessary again to start with a discussion of ontogeny. For group A it is clear that the structures are close to the original probacula pattern which is determined very early in the ontogeny in the primexine. For *Zea*, Skvarla & Larson (1966) have shown that the precise location of the probacula is induced by microtubules. The tops of the probacula often fuse more or less completely rather soon, and the resulting tectum may have a more or less open structure depending on the balance between sporopollenin deposition and rate of expansion of the exine.

Although originally probacula initiation may have resulted from a basic least surface configuration of the microtubules, in many cases further control of patterning is related to the apertures. Also, the bacula pattern itself may become reticulate or linear, forming single or multiple rows. The way in which these more specialized arrangements originate is as yet unknown.

The larger structures which develop from the tectal surface appear to be determined mainly by the underlying columellate patterns but may also follow independent least surface configurations when developing during the later phase when tapetal deposition of sporopollenin takes place, as shown for *Tagetes patula* by Heslop-Harrison (1969). This independence is especially clear in the case of some of the micro-patterns revealed by SEM. While in the case of Gramineae pollen, the pattern of suprategal spinules rather closely conforms to the underlying columellae pattern, in the case of *Plantago* their pattern is independent and closely follows a least surface configuration. In Fig. 1 this pattern is shown to develop independently of the underlying operculate aperture, as if deposited on a thin outer covering membrane. For *Myriophyllum* Aiken (1978) has shown that such a pattern indeed develops relatively late in the ontogeny. In other case the outer surface is covered with a much more dense structure. Some of these micro-patterns, like those in *Quercus coccifera* (Fig. 2), show a remarkable resemblance to patterns of coral growth such as found in the genus *Goniopora*. This is no doubt due to the fact that both processes take place in a liquid environment saturated with the dissolved building material, respectively sporopollenin and calcium carbonate, while the growth pattern of the sporopollenin receptor surfaces must be similar to that of the coral organisms, albeit on a vastly different scale. It is likely that differences in micropatterns which, as Smit (1973) has shown, characterize different groups of oaks are due to different branching patterns of the receptor molecules.

The combined structures represent a close integration of both types of processes. The best examples of this group are found in the echinate structures which have developed in such variety in many unrelated angiosperm groups.

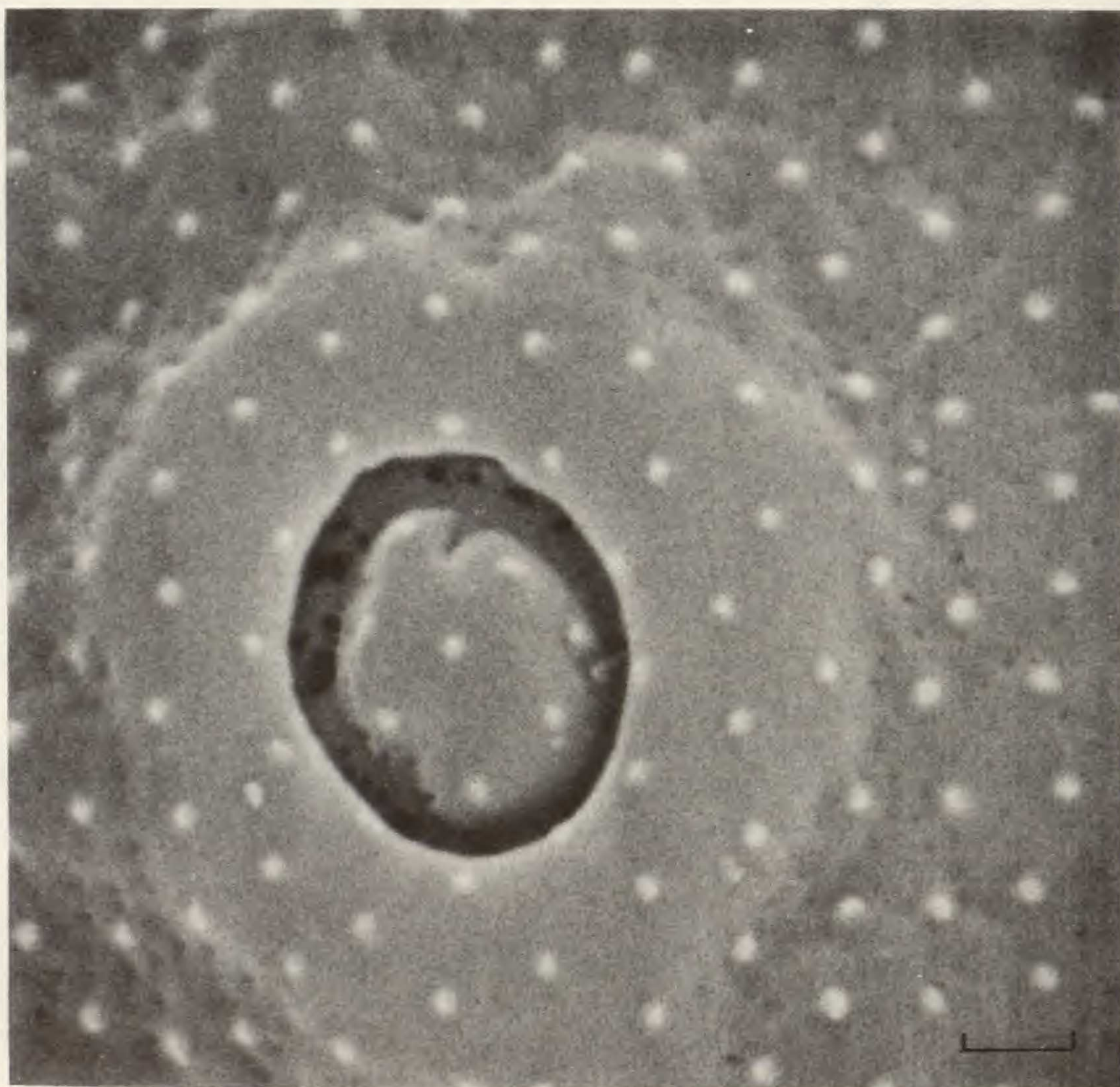


FIGURE 1. *Plantago lanceolata* (Plantaginaceae). Surface view of a pore showing operculum, invaginated and locally perforated pore membrane, and protruding annulus surrounding the pore. The outer surface of the tectum appears irregularly wavy with very fine scattered perforations, while the surface of annulus and operculum is more dense and smooth. The white dots represent a regularly spaced pattern of minute verrucae. This hexagonal pattern is independent of the underlying aperture structure. SEM, acetolyzed, 10,000 $\times$ . Courtesy Dr. C. G. S. Clarke.

In Fig. 3 some examples are given which demonstrate how various exine layers are involved. Recently Rowley & Dahl (1977) have shown in great detail the ontogeny of spine structure in *Artemisia* (Compositae). It will be clear that for such a complex chain of events to evolve, a long history starting with the simple probacula-derived pattern of early angiosperm pollen types must be postulated, and it is therefore not surprising that Compositae pollen is one of the latest pollen types to appear in the fossil record (Oligocene, cf. Muller, 1970).

Another example of an integrated structure is the exine of *Dipterocarpus*. Here tectum and columellae have been transformed into urn-shaped structures, fused into a structure of higher order with concomitant disappearance of the endexine, while the sole has been reduced from a thick solid layer to a thin laminated one (Maury et al., 1975). The ontogeny of this structure has been traced to the earliest phase of sporopollenin deposition and, as shown in Fig. 4, is already largely developed. The subsequent expansion to the mature pollen grain, shown graphically in Fig. 5, involves a 3-fold increase in size and shows how the basic

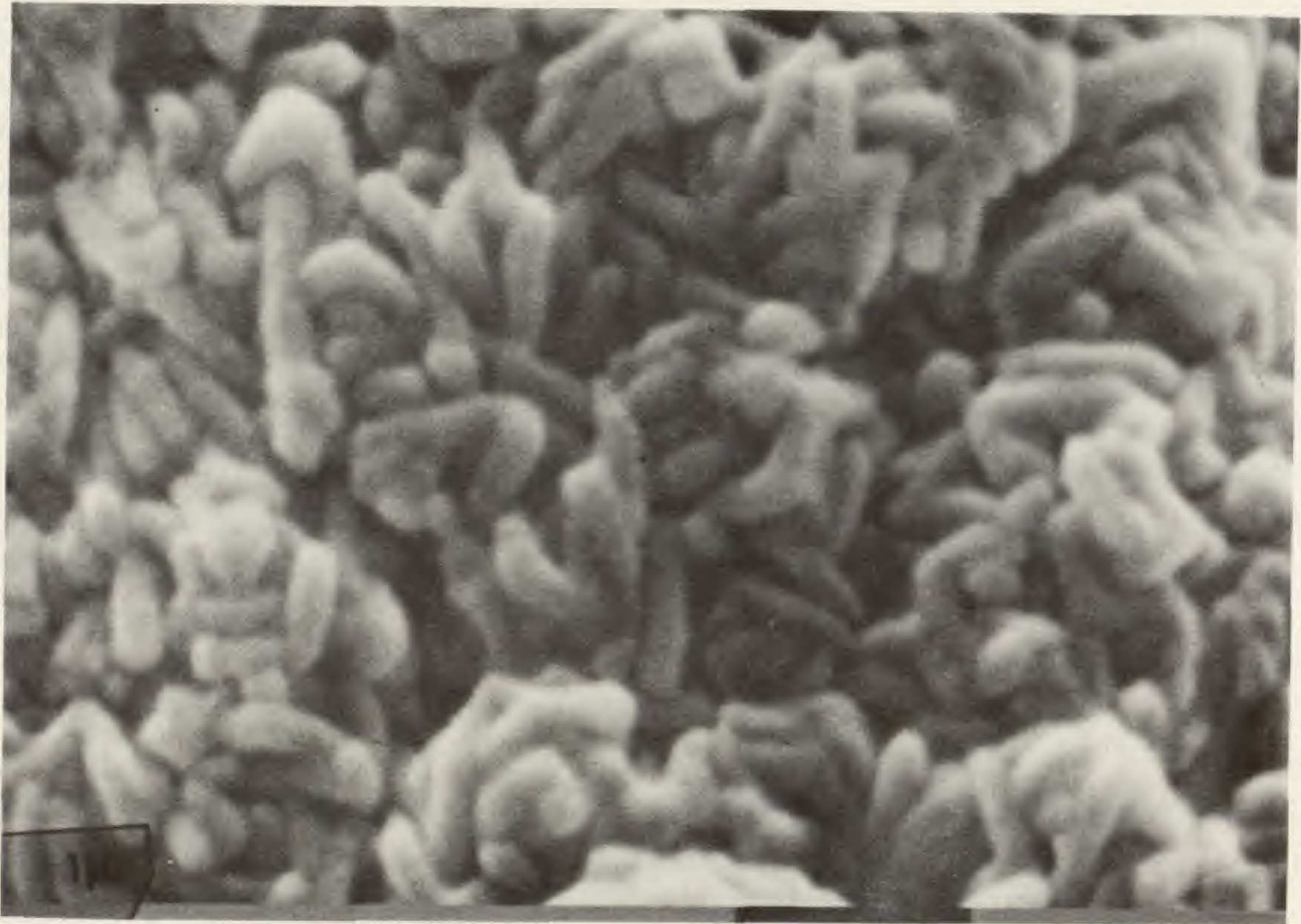


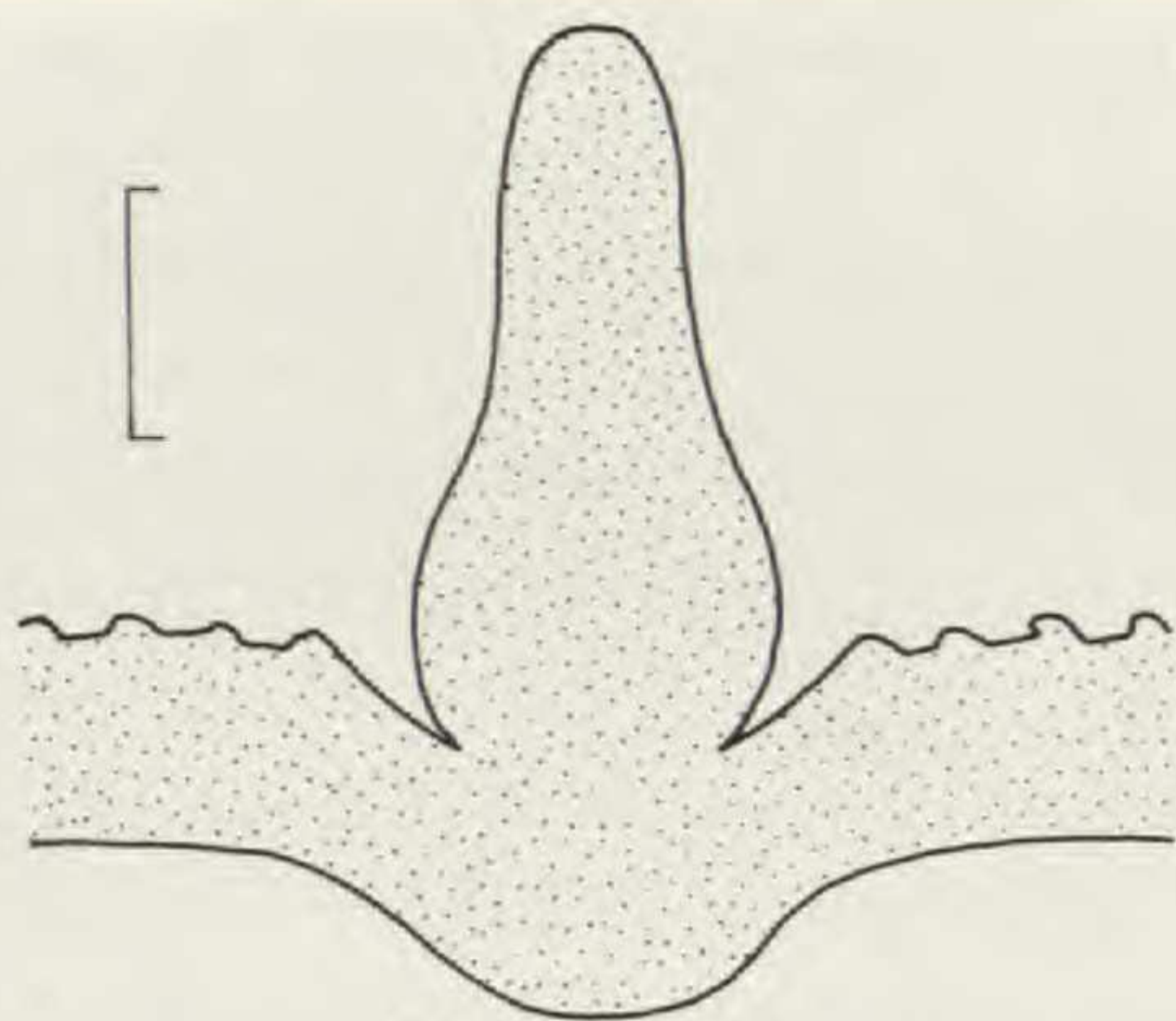
FIGURE 2. *Quercus coccifera* (Fagaceae). Surface view of extraapertural exine. The tectum is densely covered by irregular agglomerations of elongated rugulate elements. This very fine structure appears accretionary in nature and probably was deposited independent of underlying columellate patterns. SEM, acetolyzed, 20,000 $\times$ .

exine architecture is retained. The growth curve for *Dipterocarpus* pollen indicates a visco-elastic growth pattern and, exceptionally, SEM has revealed ringlike patterns, visible in Fig. 4E, which may reflect this mode of growth which is, of course, markedly different from the accretionary surface pattern referred to earlier. Many other complex exines must also be adapted to such a retention of shape during rapid growth and sporopollenin accretion. For a more detailed discussion of the processes involved, reference must be made to Heslop-Harrison (1971b: 85–86).

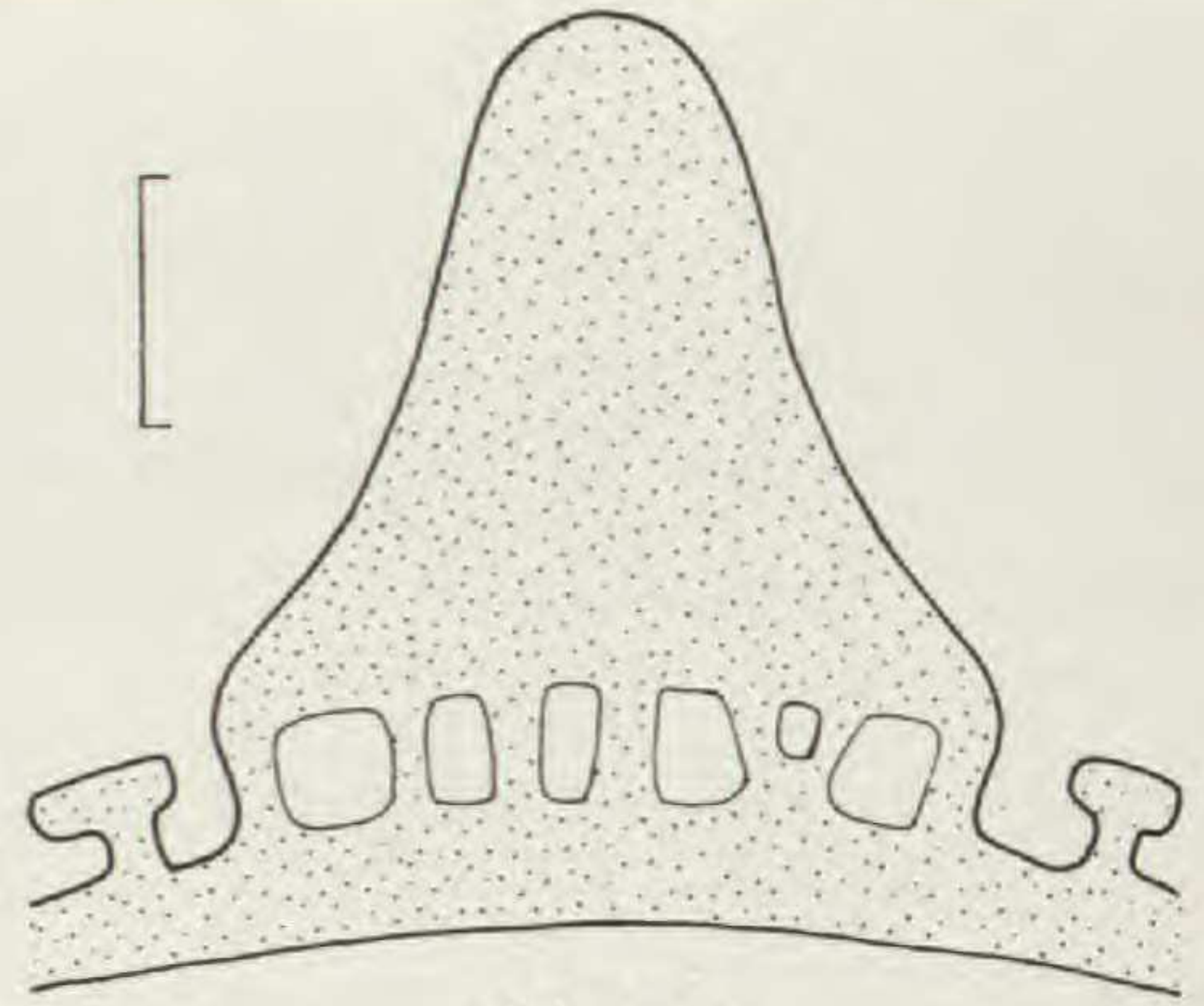
A functional analysis of the exine architecture of mature angiosperm pollen involves a study of the following aspects:

A. The protective function, mainly against adverse atmospheric conditions such as dryness and UV radiation. The original way in which the exine protects the living content may have been by a solid sheet such as is common in ferns and also in *Degeneria* and other primitive dicotyledons. In the open structures developed later, the protective function of the sporopollenin may have been partly transferred to what Heslop-Harrison (this symposium) has termed the lipid seal. In open reticulate structures the lipid layer would be retained by capillary forces.

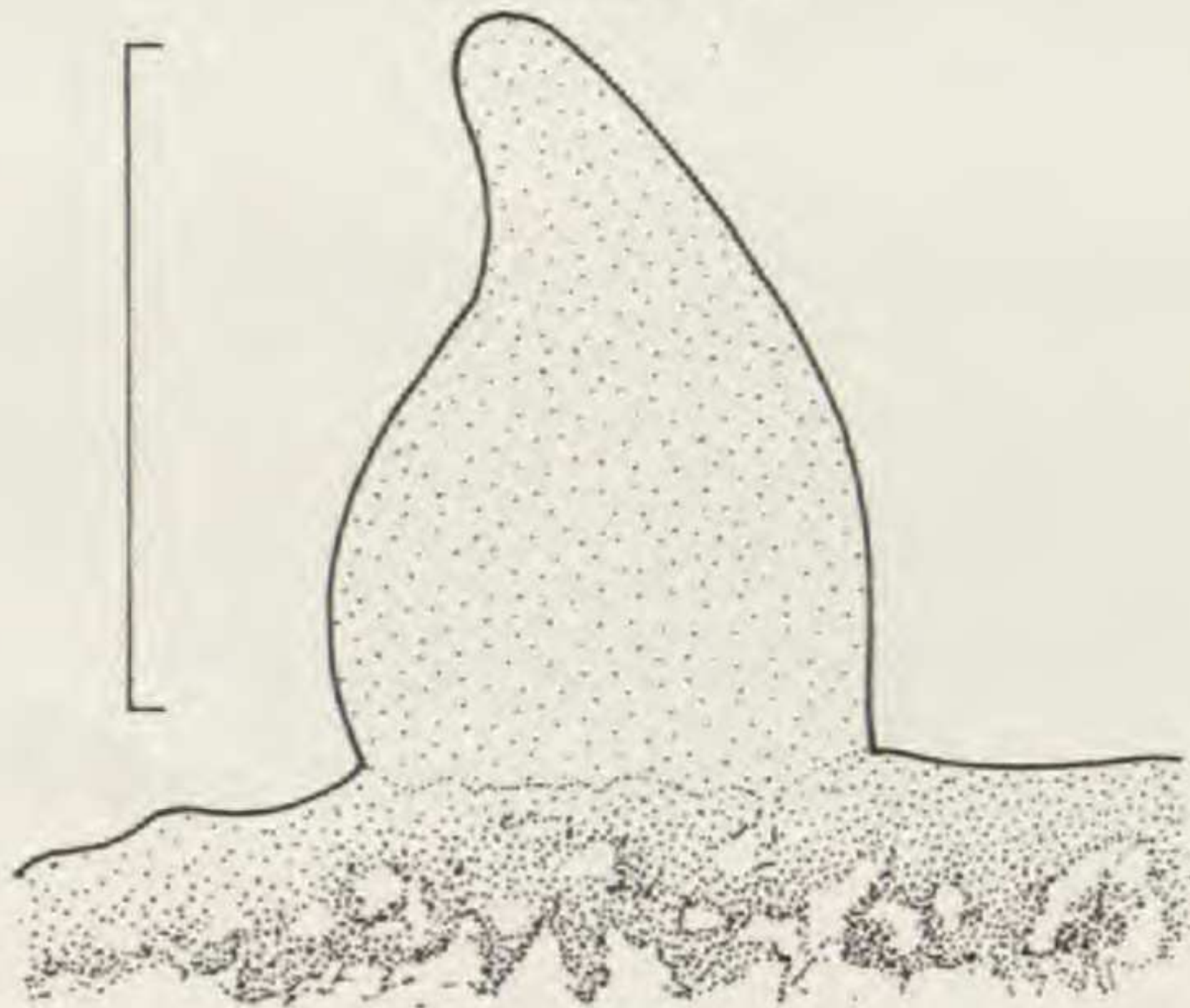
B. The harmomegathic function in the sense of Wodehouse (1935), accommodating the unavoidable changes in volume caused by fluctuations in relative humidity of the atmosphere. Special attention must be drawn here to the traumatic moment occurring during anthesis at the desiccation phase of the anthers, when the pollen grains suddenly are transferred from a liquid to an atmospheric environment. It appears likely that this is the moment of maximum stress for the



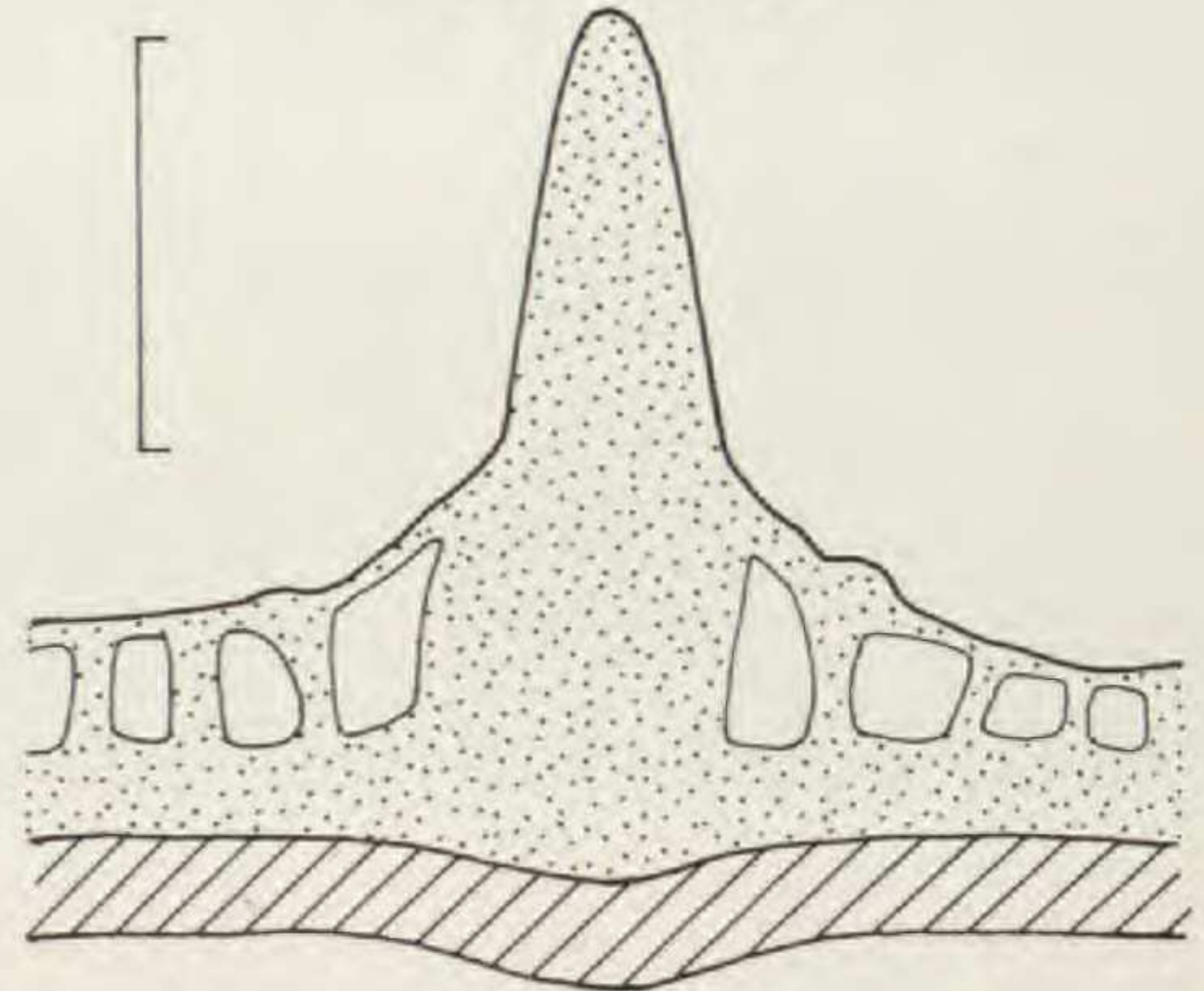
Mauritia,  
Palmae



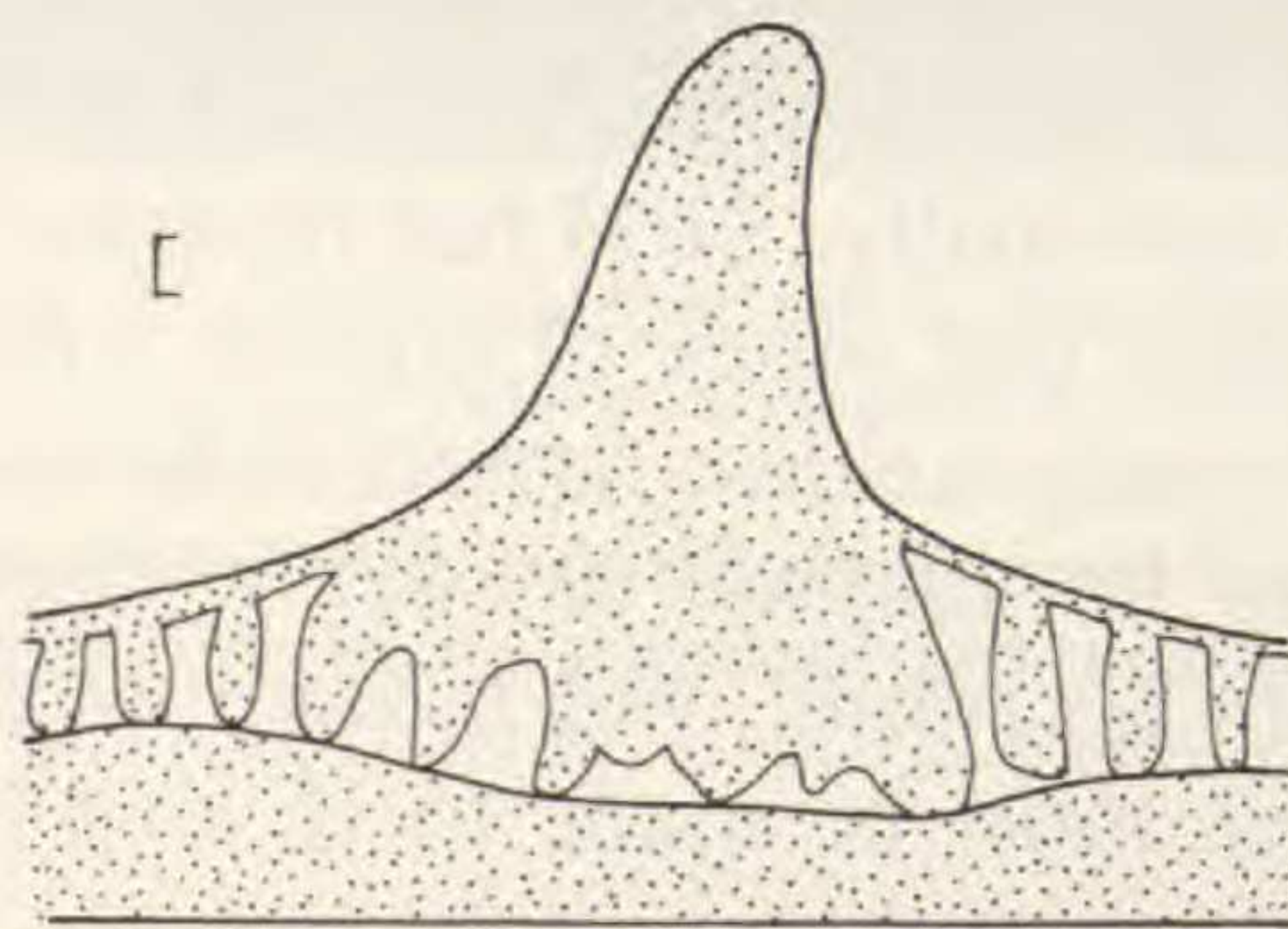
Nypa,  
Palmae



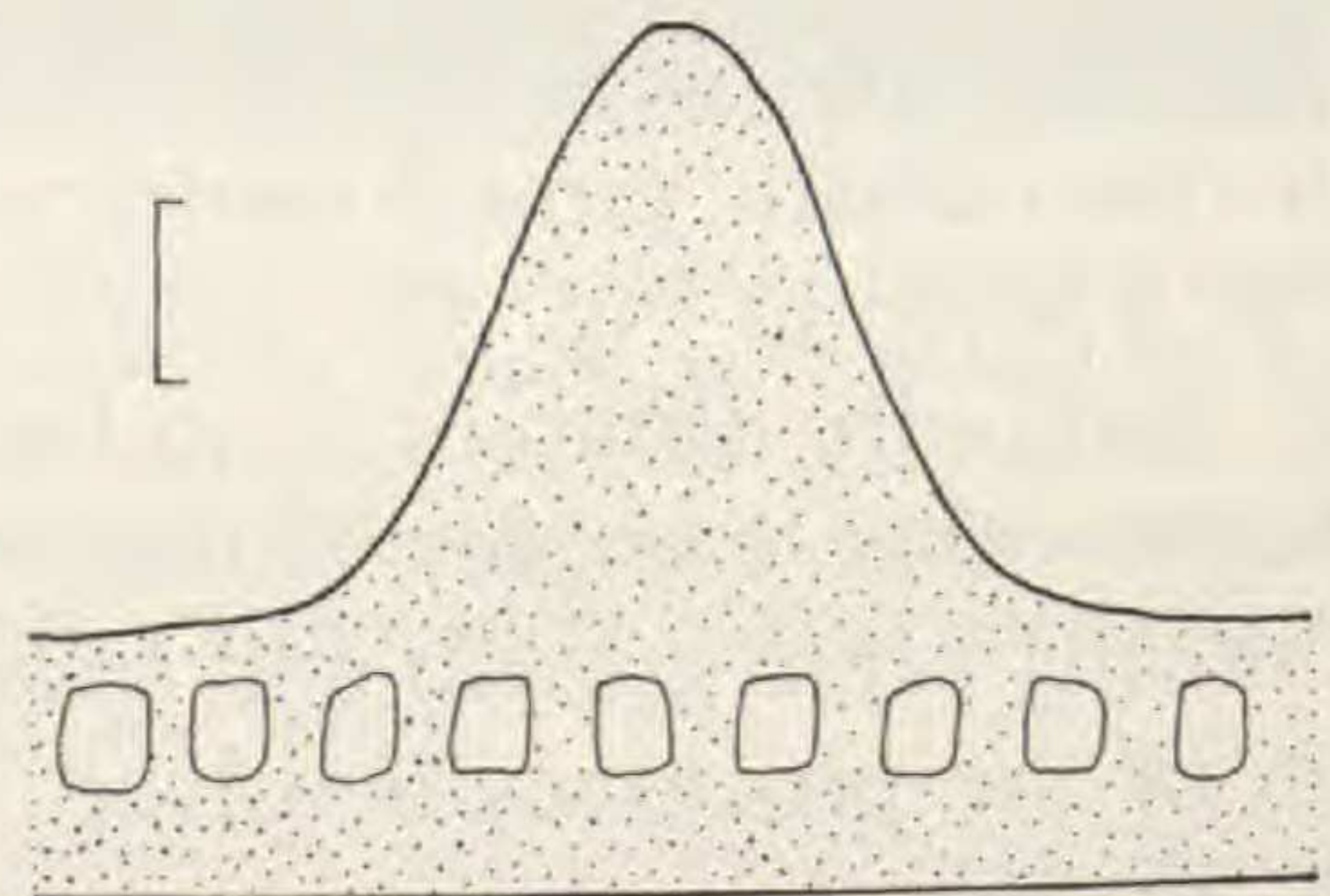
Friesodielsia,  
Annonaceae



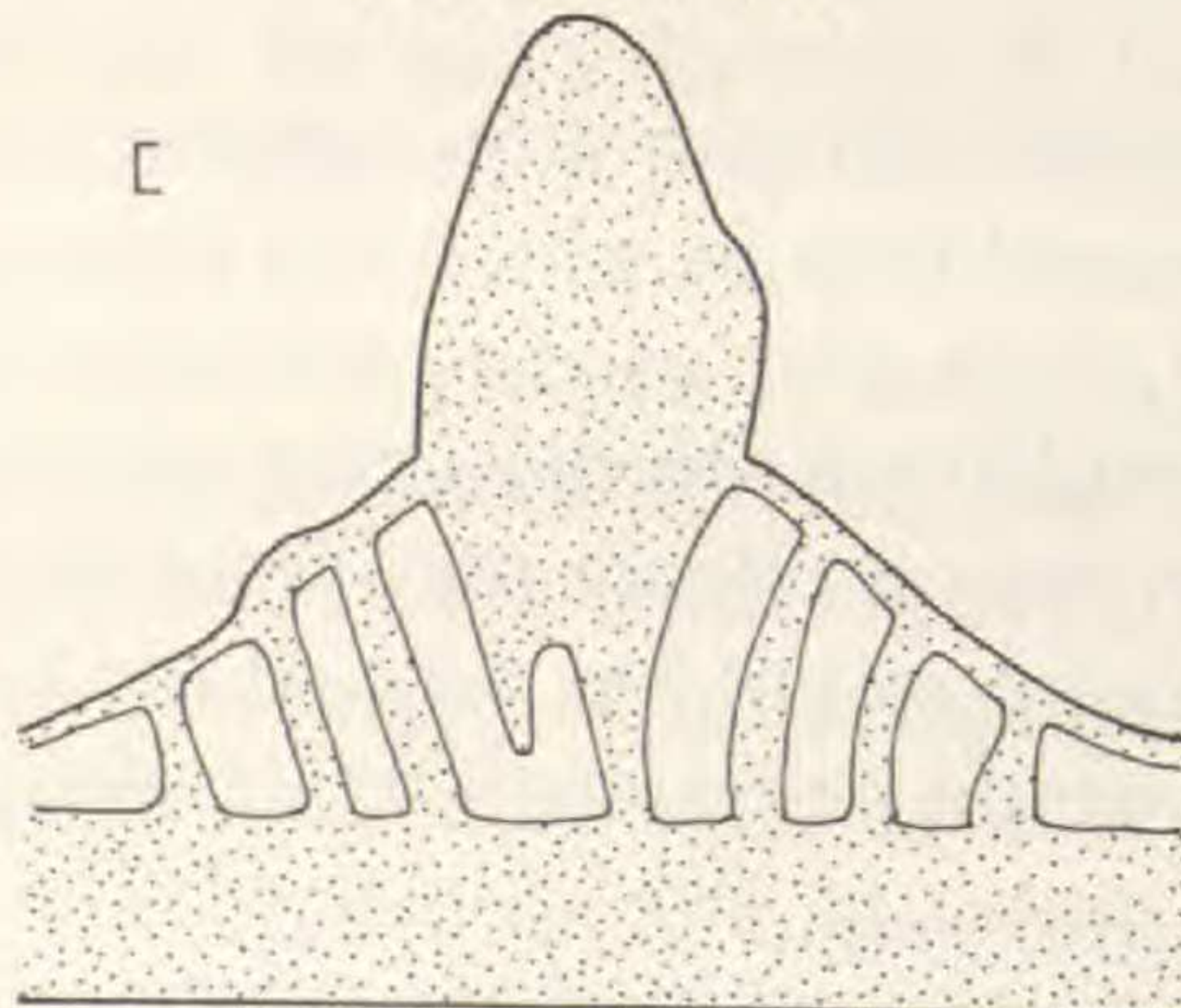
Iodes,  
Icacinaceae



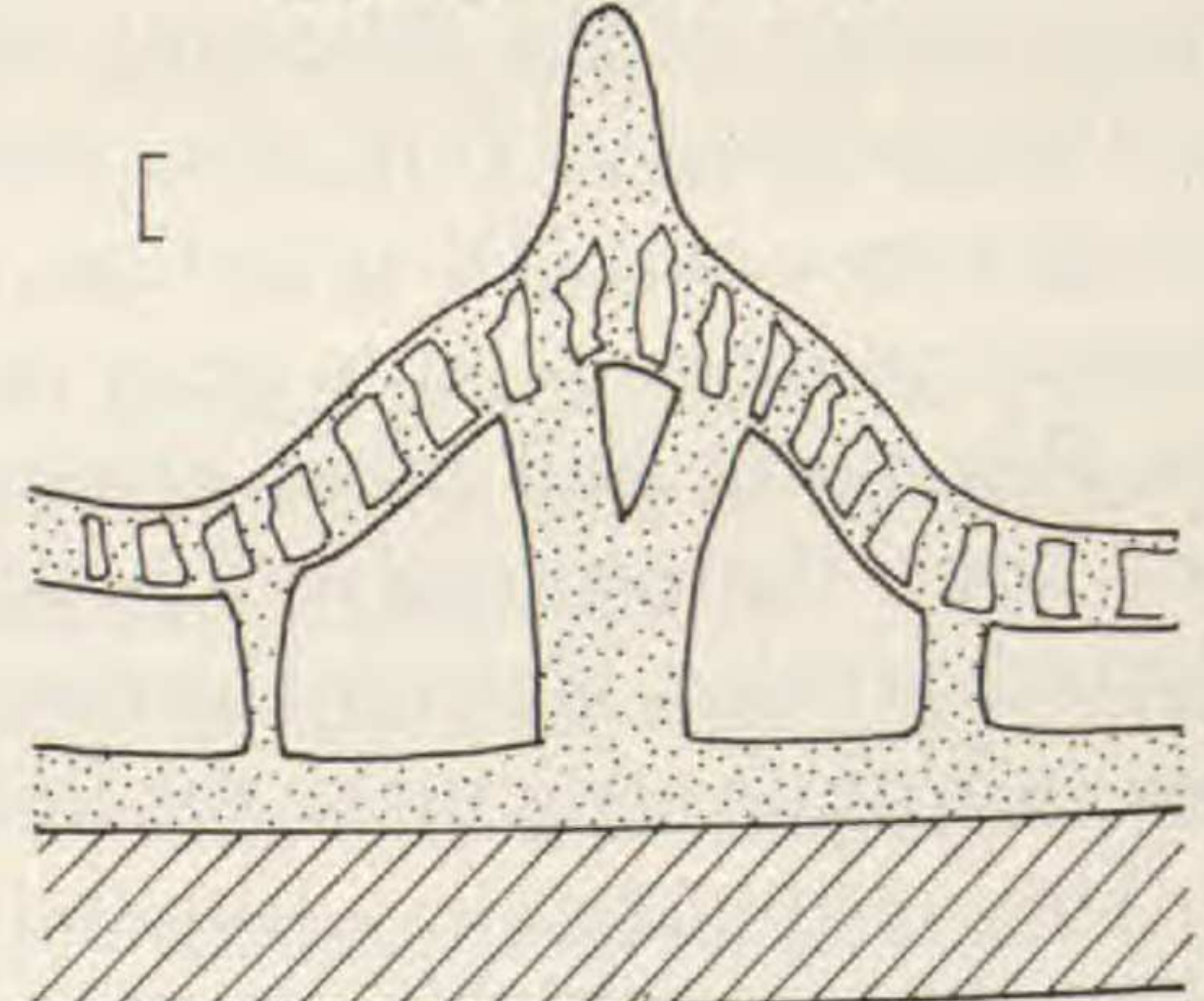
Hibiscus,  
Malvaceae




Pterospermum,  
Sterculiaceae



Ipomoea,  
Convolvulaceae



Lychnophora,  
Compositae

 ectexine


 endexine

FIGURE 3. Spine structure in angiosperm pollen. Scale: 1  $\mu$ m.

exine. It has to be strong and flexible enough to prevent collapse at this critical phase of drying out. Payne (1972) has shown the forces involved to be considerable and has argued that a large part of exine architecture has evolved in response to these factors, rightly emphasizing, however, that the pollen grain functions as a whole, apertural and extra apertural structures being closely integrated. McGlove (1978) has recently argued that the tetrad of *Epacris* functions as a single harmomegathic unit.

C. The reservoir function, stressed by Heslop-Harrison (1976), who has shown that the exine cavities are filled with many other physiologically active substances besides lipids. The storage of recognition substances here would explain the frequency of exines with an open architecture, adapted to rapid contact with the stigma, ensuring that recognition is not entirely dependent on an aperture touching the stigma surface.

Hesse (1978) has recently studied in detail these lipids which he considers to be mainly functioning as sticky "pollenkitt." Of interest is that in some pollen types with a closed tectum (*Aquilegia*, *Castanea*, *Quercus*) the intracolumellar cavities are entirely filled with lipids, while the outer surface is hardly sticky. It would appear likely that in such cases the sealing function is more significant.

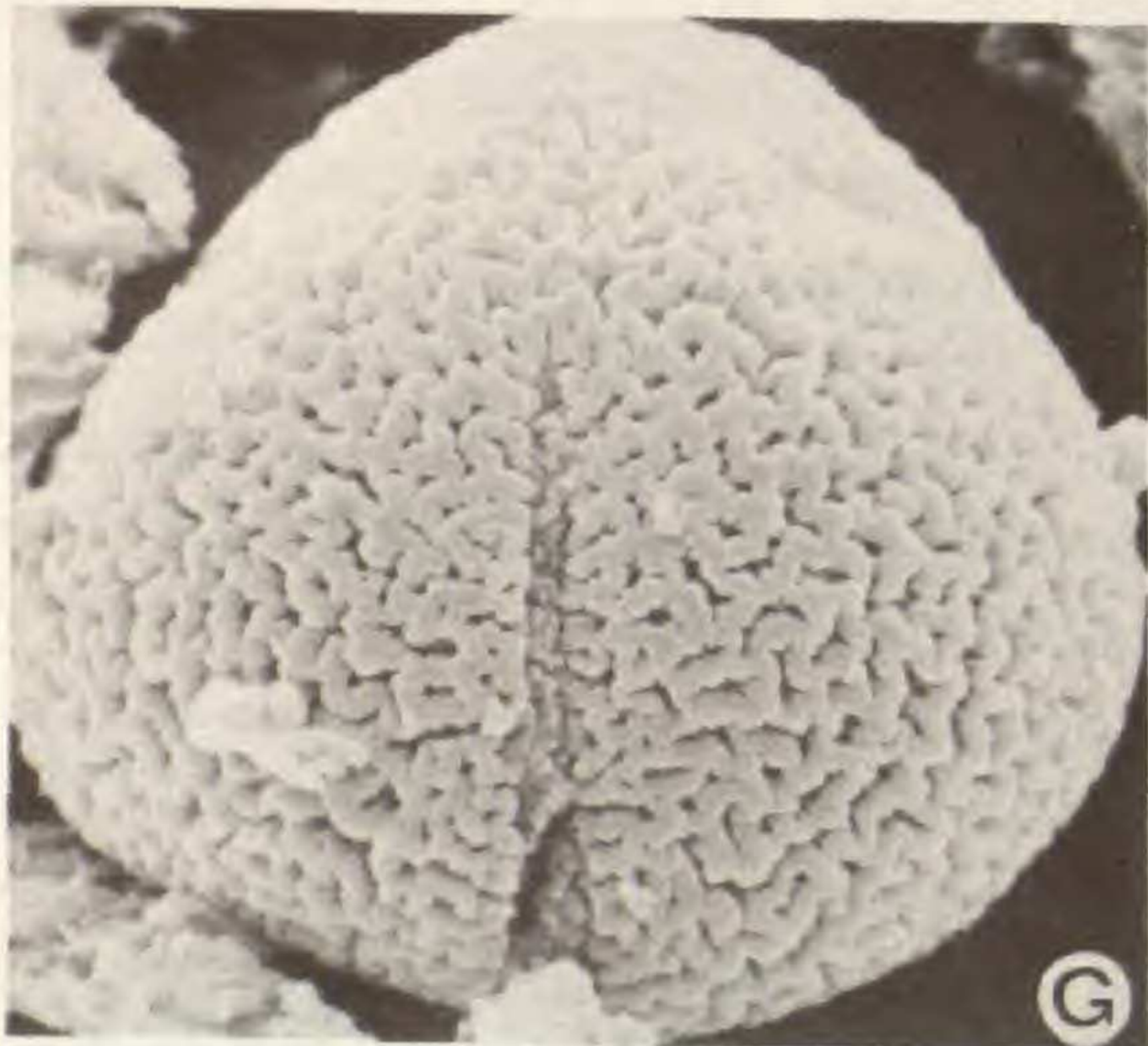
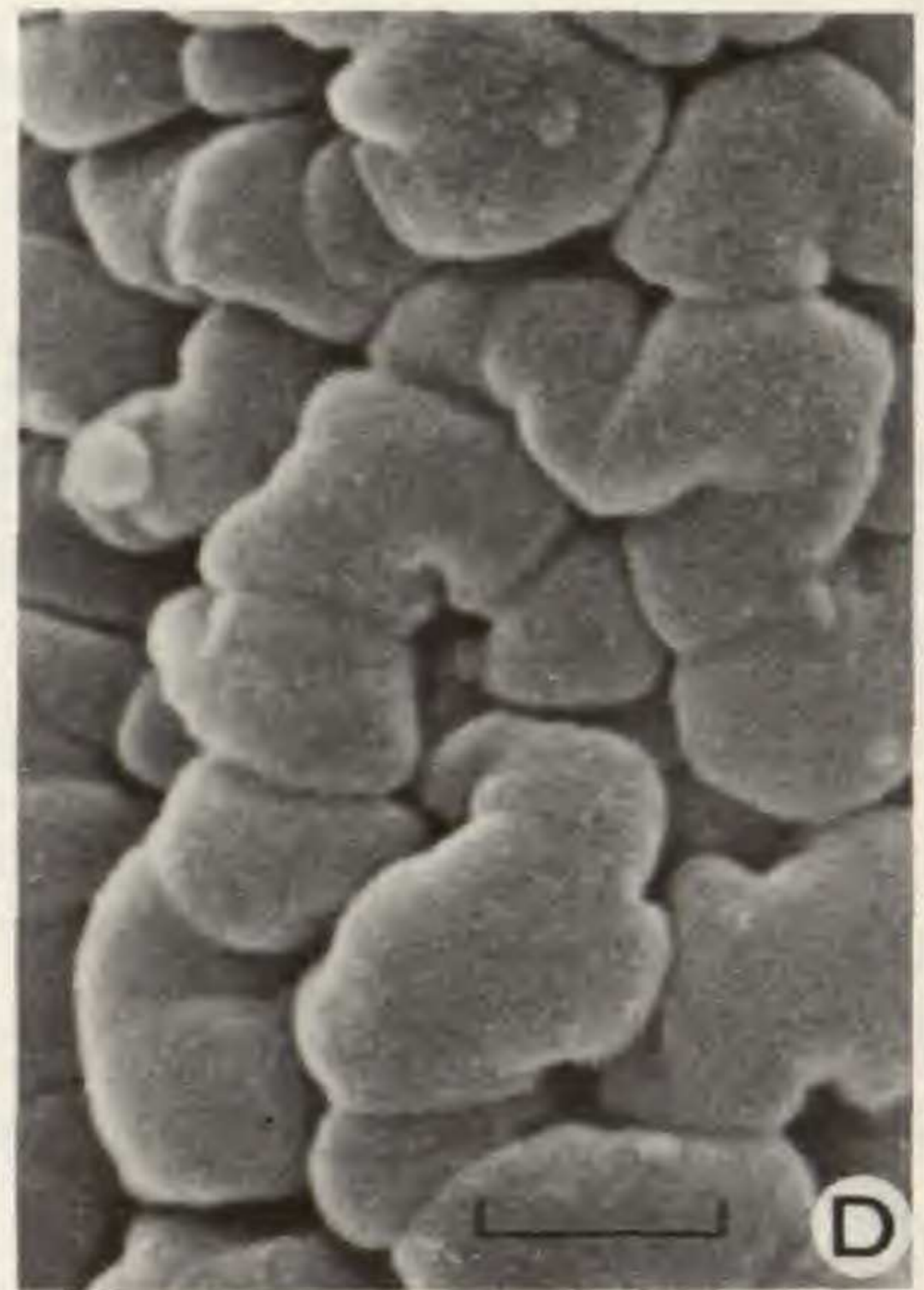
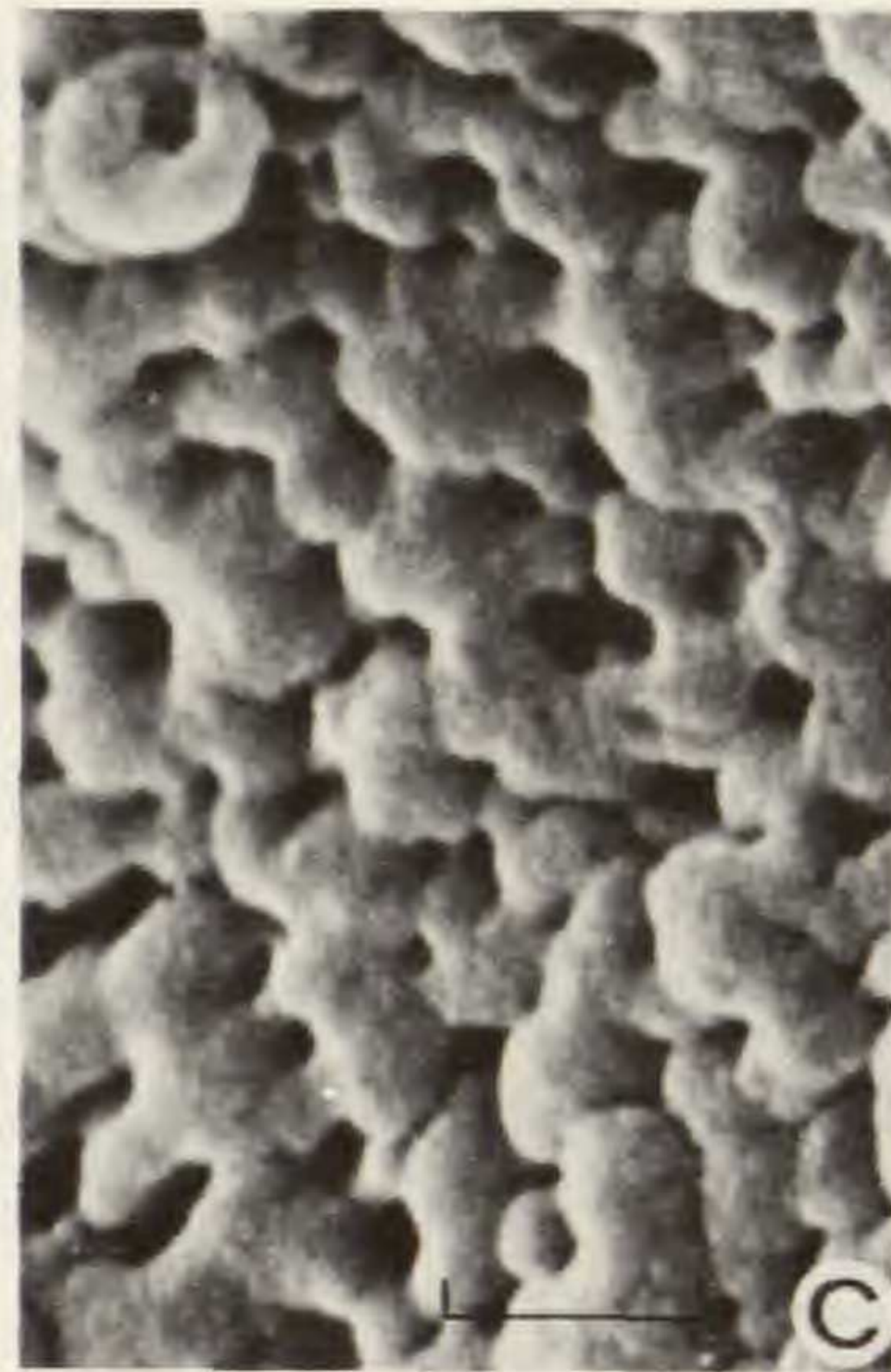
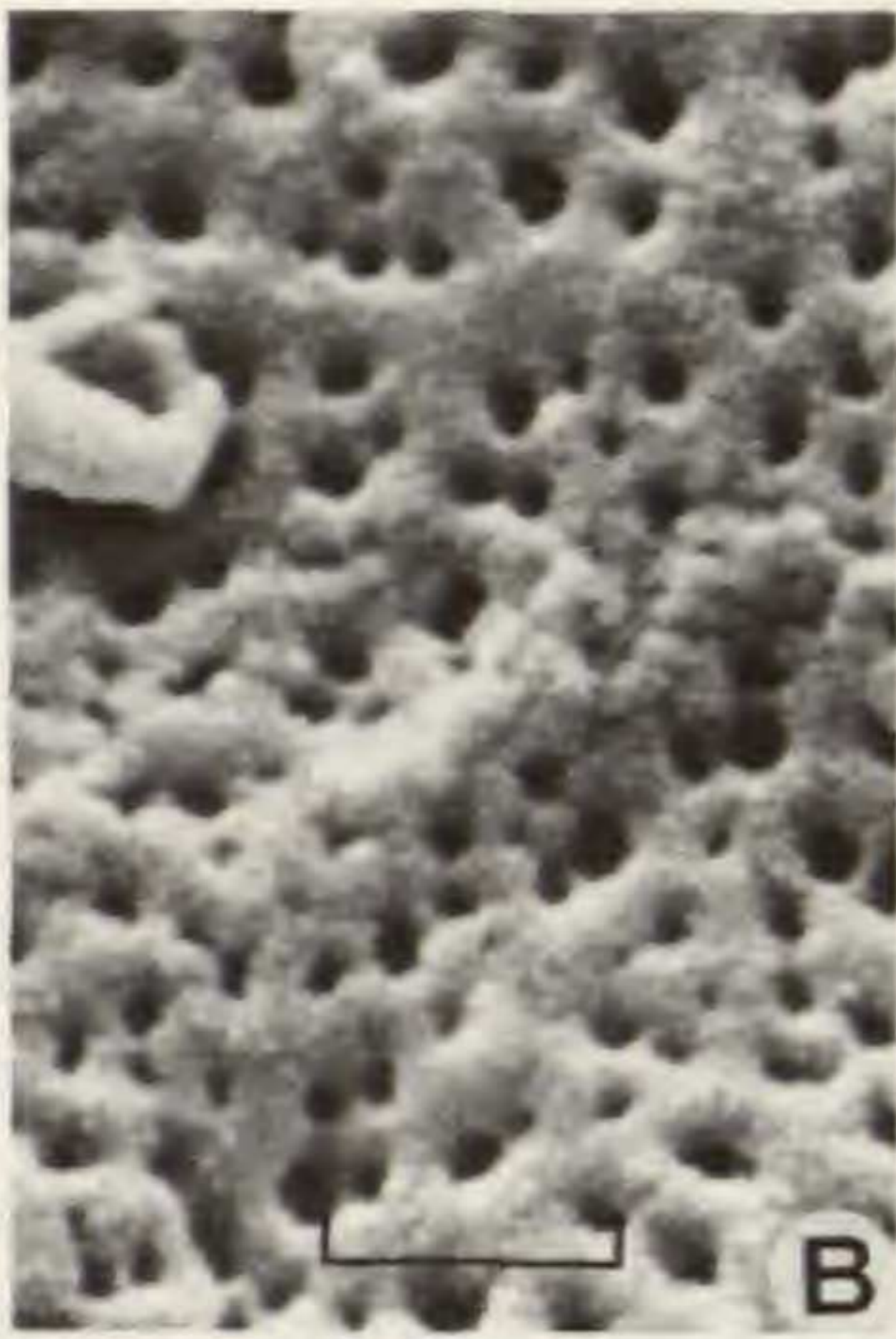
D. The clustering function, related to mode of dispersal. This aspect has early caught the attention of pollen morphologists and led to the well-known distinction of smooth-surfaced, dry pollen of wind-pollinated taxa and oily, often spinose or reticulate pollen of insect-pollinated taxa.

The significance of oily surface layers was already studied in detail by Knoll (1930) and Pohl (1929, 1937) and, as mentioned above, recently by Hesse (1978). However, it must be pointed out that certain insect-pollinated flowers have small, smooth dry pollen which is adapted to the special way in which the pollen is shaken out of the anthers through a small opening. This was already described by Troll (1928) for *Galanthus* and occurs in many other families as well. Beattie (1971) has studied the mechanism in *Viola*, while, according to Macior (1968), visiting insects often gather pollen by wing vibration from similar anther types in *Pedicularis* (Scrophulariaceae) and *Dodecatheon* (Primulaceae).

#### SHAPE

Distally monosulcate angiosperm pollen grains, such as those of *Magnolia*, have generally retained the typical elongated boatshape found, for example, in *Cycas* and other gymnosperms. However, rather early in the fossil record and especially in the *Clavatipollenites* lineage, a tendency towards a more spherical shape becomes manifest. With the origin of the tricolpate type, formed in a tetrahedral tetrad, a basically spherical shape develops which can subsequently be modified by differential growth in an equatorial, polar, or interapertural direction leading to oblate, prolate, or trilobate shapes, respectively. These shape modifications are often closely integrated with apertural and structural modifications.

It is considered likely that the change in shape was primary and that the change from a single slitlike sulcus to the tricolpate condition was secondary. This is suggested by the circumstance that a single inwardly folding sulcus on a boat-shaped grain forms a well-integrated harmomegathic system, while the same aperture on a sphere creates unequal harmomegathic stresses which can only be



equalized by shortening of the slit with, as logical end-product, a single round pore. However, this entails a reduction of the germinative area and the development of the tricolpate type may be seen as the achievement of both a more efficient harmomegathic stress pattern with a better relation between volume reduction and stress distribution and an increase in germinative area, promoting fast and efficient stigmatic contact.

A major part of the subsequent evolution of the tricolpate type consists of further specialization towards controlled harmomegathy and the shape modifications can be related to this. In the first place the relative increase of growth of the polar axis, the trend towards longiaxy, can be seen as a recreation of the elongated shape, to which, as pointed out earlier, the colpate aperture is best adapted. Compared to the boat-shaped sulcate type, the orientation of the long axis is changed from equatorial towards polar.

The opposite trend towards relative shortening of the polar axis, the trend towards breviaxy (Van Campo, 1966), is also widespread and, as mentioned before, generally associated with a striking modification of the apertural system. In extreme cases this leads to the reduction of the ectocolpi and the development of porate apertures. The shape is often further modified in a triangular one with pores at the angles or interangular. In such pollen types the disappearance of the colpi means a transfer of the harmomegathic function from the colpi to different exine structures, examples of which will be discussed later on.

#### SIZE

Wodehouse (1935) has shown in an excellent way how transport conditions often limit the size of angiosperm pollen grains. The majority fall in the 20–40  $\mu\text{m}$  range and are adapted to easy liberation from the anthers, moderate wind transport, and optimal adherence both to insect vectors and to the stigma. The typically wind-pollinated grains also fall in this range. Exceptions are the large pollen grains, mostly transported by animal pollinators, and the very small ones which are often associated with highly specialized pollination systems. In rare cases such as the paper mulberry, vividly described by Wodehouse (1935), an explosive device liberates the extremely small pollen grains. Gehrman (1911)

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FIGURE 4. Exine growth in *Dipterocarpus* (Dipterocarpaceae).—A–C: *D. gracilis*.—D–E, G: *D. nudus*.—F: *D. confertus*.—A. Early stage showing partly doubled-up exine with urn-shaped invaginations (arrows) without any distinction between columellae and tectum. The laminated basal layer or sole(s) is still very thin and loosely attached to the invaginations. TEM, glutaraldehyde-OsO<sub>4</sub> fixation, stained with uranyl acetate and Reynold's lead citrate, 20,000 $\times$ .—B. Very early stage. Exine surface rather flat with a granular structure and scattered perforations. At top left, urn-shaped Ubisch body. SEM, acetolyzed, 10,000 $\times$ .—C. Early stage, probably corresponding to A. The exine surface starts developing the convoluted ridge system. At top left, another Ubisch body. SEM, acetolyzed, 10,000 $\times$ .—D. Middle stage, with strongly convoluted and compressed exine ridges hiding the urn-shaped depressions and with an indistinctly finely striated surface. SEM, acetolyzed, 10,000 $\times$ .—E. Mature stage, showing fully expanded exine, exposing the depressions and occasional bridging lower ridges. Surface of exine clearly finely striated probably resulting from sporopollenin accretion on an irregularly stretching exine. SEM, acetolyzed, 10,000 $\times$ .—F. Sectioned exine showing the urn-shaped invaginations to the bases of which the thin basal layer is attached. SEM, acetolyzed, 4,200 $\times$ .—G. Mature grain showing the uniform exine pattern and the narrow colpus which will only invaginate slightly. SEM, acetolyzed, 1,000 $\times$ .

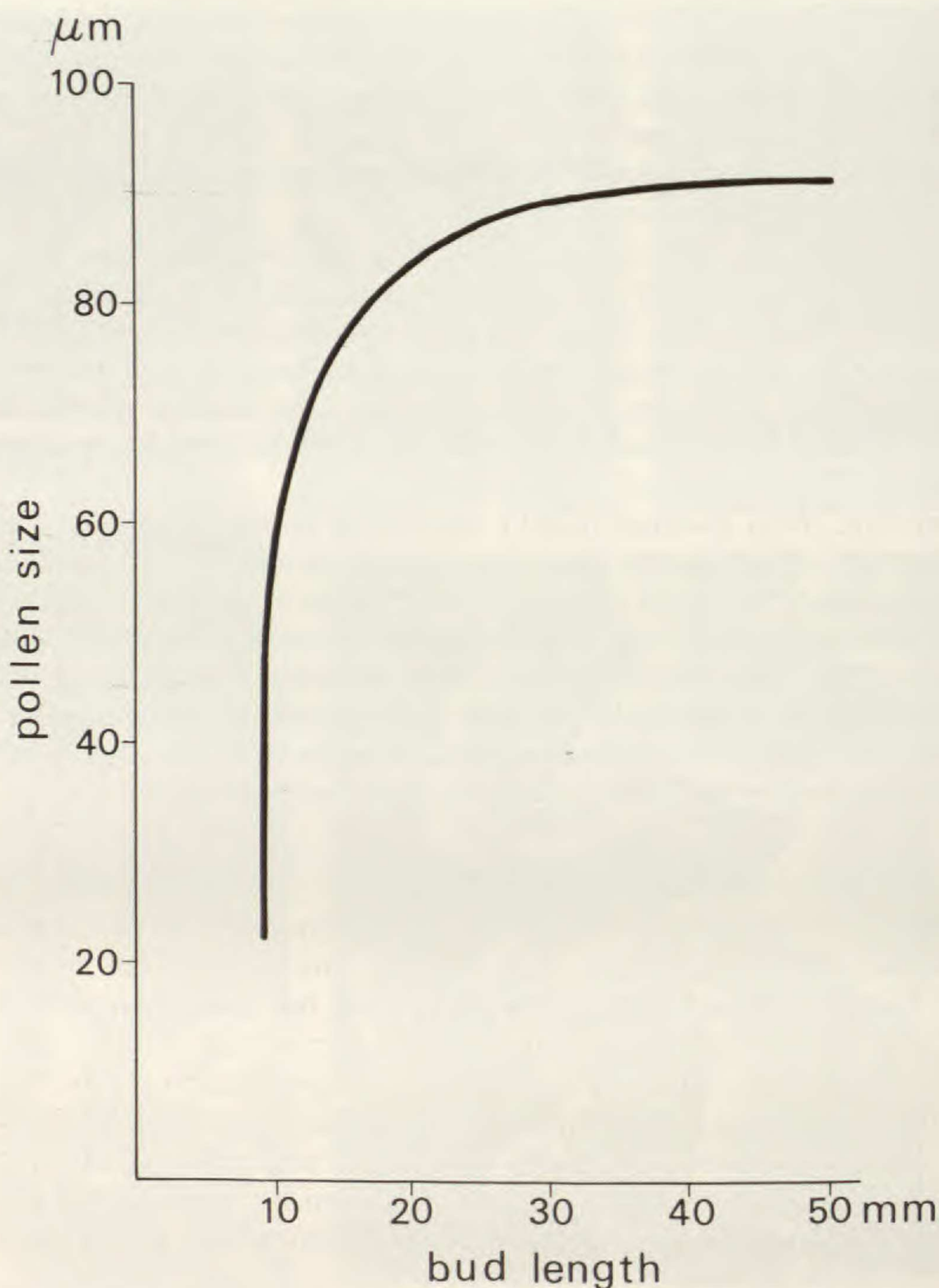


FIGURE 5. *Dipterocarpus caudiferus* (Dipterocarpaceae). Growth curve of acetolysis resistant exine.

had already described a similar mechanism for *Bruguiera* (Rhizophoraceae; cf. also Tomlinson, 1977).

Whitehead (1969) has discussed in more detail the significance of pollen size for wind-pollinated plants by considering aerodynamic principles. He emphasized that very small grains ( $<20 \mu\text{m}$ ), although dispersed widely, cannot be captured efficiently by the stigma, unless it is thinly branched like in grasses.

Wodehouse (1935) also pointed out that primary evolutionary changes in size may have profound influences on exine morphology: the smaller the pollen grain, the less complex architecture and aperture structure.

In this connection attention must be drawn to the relatively small size of many



TABLE 1. Relation of chromosome number with pollen size.

+ Correlation			No Correlation		
A, Intraspecific	B, Interspecific	C, Inter-generic	A, Intra-specific	B, Interspecific	C, Intergeneric
Campanulaceae, <i>Campanula patula</i> , 1; <i>C. rotundifolia</i> , 1; <i>Lobelia siphilitica</i> , 2.	Labiatae, <i>Monarda fistulosa</i> , 2; <i>Salvia pratensis</i> , 2; <i>S. splendens</i> , 2.	Campanulaceae, <i>Campanula</i> , 1.		Dipterocarpaceae, <i>Shorea</i> , 14; <i>Hopea</i> , 14.	Acanthaceae, 18.
Compositae, <i>Cichorium intybus</i> , 3; <i>Thelesperma</i> sp., 4; <i>Tridax coronipifolia</i> , 4.	Leguminosae, <i>Trifolium hybridum</i> , 2; <i>T. incarnatum</i> , 2; <i>T. pratense</i> , 2; <i>T. repens</i> , 2.	Compositae, <i>Thelesperma</i> , 4.		Onagraceae, <i>Gayophytum</i> , 15.	Dipterocarpaceae-Dipterocarpoideae, 14.
Cruciferae, <i>Arabidopsis thaliana</i> , 5; <i>Brassica oleracea</i> , 3; <i>B. rapa</i> , 3; <i>Raphanus sativus</i> , 3; <i>Sinapis alba</i> , 3.	Polygonaceae, <i>Rumex patientia</i> , 3.	Gramineae, <i>Aira</i> , 21; <i>Andropogon</i> , 11; <i>Avenella</i> , 21; <i>Deschampsia</i> , 21.		Solanaceae, <i>Nicotiana</i> , 16.	Gramineae-Deschampsiiinae, 21.
Gramineae, <i>Aristida purpurea</i> , 22; <i>Bouteloua curtispindula</i> , 23; <i>Poa pratensis</i> , 24.	Ranunculaceae, <i>Caltha palustris</i> , 7.	Hydrophyllaceae, <i>Phacelia</i> , 6.		Sonneratiaceae, <i>Sonneratia</i> , 17.	Meliaceae, 20.
Hydrophyllaceae, <i>Phacelia corymbosa</i> , 6; <i>P. imbricata</i> , 6; <i>P. mutabilis</i> , 6; <i>P. nemoralis</i> , 6.	Rosaceae, <i>Sanguisorba minor</i> , 8; <i>S. officinalis</i> , 8.	Plantaginaceae, <i>Plantago</i> , 12.			
	Rubiaceae, <i>Oldenlandia corymbosa</i> , 9.	Polemoniaceae, <i>Phlox</i> , 13.			
	Scrophulariaceae, <i>Digitalis ambigua</i> , 3; <i>D. lanata</i> , 3; <i>D. lutea</i> , 3.				
	Solanaceae, <i>Datura stramonium</i> , 2; <i>D. tatula</i> , 2; <i>Nicotiana silvatica</i> , 2; <i>N. trigonophylla</i> , 2.				
	Umbelliferae, <i>Sanicula crassicaulis</i> , 10.				
References:	1. Gadella, 1964	7. Smit, 1968	13. Taylor & Levin, 1975	19. Leuenberger, 1976	
	2. Maurizio, 1956	8. Erdtman & Nordborg, 1961	14. Muller, 1979	20. Pennington & Styles, 1975	
	3. Schwanitz, 1950	9. Lewis, 1964	15. Lewis & Szweykowski, 1964	21. Albers, 1975	
	4. Kessler & Larson, 1969	10. Bell, 1954	16. Pandey, 1971	22. DeLisle, 1970	
	5. Bronckers, 1963	11. Gould, 1957	17. Muller, 1969	23. Kapadia & Gould, 1964	
	6. Heckard, 1960	12. Bassett & Crompton, 1968	18. Raj, 1961	24. Nissen, 1950	

TABLE 2. Influence of external factors on pollen size.

Environmental Factors	+ Correlation	No Correlation
Light Intensity	Fagaceae, <i>Castanea</i> , 1.	
Temperature	Compositae, <i>Xanthium</i> , 2. Solanaceae, <i>Lycopersicon</i> , 2.	
Temperature and Humidity		Begoniaceae, <i>Begonia</i> , 7. Gesneriaceae, <i>Saintpaulia</i> , 7. Labiatae, <i>Coleus</i> , 7.
Water	Lythraceae, <i>Lythrum</i> , 3. Umbelliferae, <i>Sanicula</i> , 4.	
Root Crowding	Umbelliferae, <i>Sanicula</i> , 4.	
Mineral Nutrition	Alliaceae, <i>Allium</i> , 4. Compositae, <i>Helianthus</i> , 4. Cruciferae, <i>Sinapis</i> , 4. Cucurbitaceae, <i>Citrullus</i> , 4. Fagaceae, <i>Nothofagus</i> , 5. Gramineae, <i>Triticum</i> , 6; <i>Zea</i> , 4. Lythraceae, <i>Lythrum</i> , 3. Portulacaceae, <i>Portulaca</i> , 4. Solanaceae, <i>Lycopersicon</i> , 4; <i>Petunia</i> , 4. Umbelliferae, <i>Daucus</i> , 4.	

## References:

- |                           |                       |
|---------------------------|-----------------------|
| 1. Oner & Planchais, 1976 | 5. Harris, 1956       |
| 2. Kurtz & Liverman, 1958 | 6. Wagenitz, 1955     |
| 3. Schoch-Bodmer, 1940    | 7. Hebda & Lott, 1973 |
| 4. Bell, 1959             |                       |

of the early Cretaceous angiosperm pollen types with indeed a simple morphology. It is only in the middle and late Cretaceous that larger, more complex pollen types start appearing. It appears probable that this increase in size was primarily caused by increased adaptation to different systems of animal pollination.

However, transport conditions are not the only factors known to be correlated with pollen size. Also, level of polyploidy may express itself directly in pollen size, the higher the level the larger the grain. In Table 1, cases described in the literature are presented grouped according to taxonomic level. It is clear that the effect is most noticeable at the intraspecific level, less apparent at the interspecific level, while at the intergeneric level no correlation is known. This suggests that the influence of polyploidy on pollen size is minor, evolutionarily short-lived, and, apparently, easily overridden by quite different selective processes.

Some of the factors known to influence pollen size in the living plant are listed in Table 2, from which it is apparent that mineral nutrition is the single most important factor directly causing variation in pollen size. This fact is significant when considering Table 3 in which the correlation between flower characters and pollen vector with pollen size are listed. A first thing which is obvious is that, contrary to the evidence for correlation with ploidy level, no cases of intraspecific correlation are shown, but this is obviously a reflection of the rarity of intraspe-

TABLE 3. Relation of flower characters with pollen size.

	+ Correlation			No Correlation		
	A, Intraspecific	B, Interspecific	C, Intergeneric	A, Intra-specific	B, Inter-specific	C, Inter-generic
Flower Size		Dipterocarpaceae-Dipterocarpoideae, 2. Fouquieriaceae, 3. Fumariaceae, <i>Corydalis</i> , 1. Papaveraceae, <i>Meconopsis</i> , 1. Tamaricaceae, <i>Tamarix</i> , 4.	Dipterocarpaceae-Dipterocarpoideae, 2. Cactaceae, 10. Fumariaceae, 1. Polemoniaceae, 7. Sonneratiaceae, 6.		Solanaceae, <i>Nicotiana</i> , 9.	
Anther Length	Papaveraceae, <i>Platystemon californicum</i> , 1.	Papaveraceae, <i>Argemone</i> , 1; <i>Glaucium</i> , 1.				
Filament Length		Bromeliaceae, 5.				
Style Length		Polemoniaceae, <i>Phlox</i> , 6. Verbenaceae, <i>Glandularia</i> , 7.				Sonneratiaceae, 11. Verbenaceae, 12.
Fruit Size		Araliaceae, <i>Tetraplasandra</i> , 8.				
Pollen/Ovule Index		Solanaceae, <i>Nicotiana</i> , 9.				
Pollen vector Size			Polemoniaceae, 6.			Sonneratiaceae, 11.
References:						
	1. Layka, 1976a, 1976b	4. Baum, Bassett & Crompton, 1971	7. Schnack & Covas, 1945	10. Leuenberger, 1976		
	2. Muller, 1979	5. Ehler & Schill, 1973	8. Tseng, 1971	11. Muller, 1969		
	3. Henrickson, 1967	6. Taylor & Levin, 1975	9. Pandey, 1971	12. Covas & Schnack, 1945		

cific differences in the characters listed. (The special case of stylar dimorphism has been excluded.) On the other hand, some clear cases of correlation at the intergeneric level in different families suggest that we deal here with important adaptive features.

For Dipterocarpaceae it has been argued (Muller, 1979) that the correlation between flower size and pollen size reflects differences in nutrient supply which are ultimately determined by selection for larger fruits. However, recent evidence (Ashton, pers. comm.) suggests that vector size may be involved also because, although the small-flowered Dipterocarpoideae are pollinated by thrips, the larger-flowered species are also visited by larger insects.

For the other cases listed of a possible correlation between flower size and pollen size, an explanation on the basis of different nutrition supply may also be the simplest one, but each case would have to be investigated in detail to rule out other causes. In *Tetraplasandra* (Araliaceae) Tseng (1971) has established a correlation with fruit size, comparable to the situation in Dipterocarpoideae. Although the correlation between pollen size and filament length reported for Bromeliaceae may be a similar phenomenon, the correlation between pollen size and style length falls in a different category altogether. This is because the style has to be penetrated by the pollen tube and this causes a built-in selective advantage for larger pollen grains with larger food reserves. Considering this, it seems surprising that only two cases of a positive correlation have been described, both at the interspecific level, while the cases of no correlation are probably more common than suggested. This emphasizes that genetic variability in size within a species may be limited by many other selective factors. In Sonneratiaceae, for instance, the genus *Duabanga* has much smaller pollen grains than *Sonneratia*, while style length is approximately equal. Moreover, both genera are bat-pollinated, hence absence of correlation with vector size. What is different, however, is the size of the flowers. In *Duabanga* the smaller flowers develop in more strongly branched inflorescences than is the case for the larger-flowered species of *Sonneratia*. This suggests, as for Dipterocarpoideae, the dominant influence of nutrition.

A relation between pollen size and vector size is indicated clearly only for Polemoniaceae. Although it is probable, as Heinrich & Raven (1972) have argued, that the energy balance of pollinators is partly affected by the amount and, presumably, size of the pollen gathered for food, it is perhaps more likely that the large showy flowers of these plants develop large pollen as a purely nutritional side effect. In fact, as Lee (1979) has pointed out, there may exist a close interrelation between flower size, style length, vector size, and pollen size.

A relation of a completely different character is shown by the pollen/ovule index and pollen size. For *Nicotiana* Pandey (1971) has found that self-compatible species or varieties of this genus have a lower ratio between the number of pollen grains and the number of ovules per flower than self-incompatible species and that the latter all have smaller pollen. Apparently, in self-compatible species fewer pollen grains are needed for fertilization, and, in consequence, more nutrients per pollen grain are available, leading to larger pollen size. Pandey (1971) also stressed that in *Nicotiana* pollen size is not directly related to chromosome number nor to size of flowers, and, in fact, the species with the largest flower

has small pollen grains. Reproductive economy thus appears to be the main determining factor here, and this may very well be of more general occurrence. It would be worthwhile to investigate this in more detail for related dioecious and monoecious species.

Still more different is the correlation with climate reported for *Ilex* by Lobreau-Callen (1975). In this genus, pollen size increases interspecifically both with altitude and latitude from which a correlation with climatic factors can be postulated. Earlier Cain & Cain (1948) reported a similar phenomenon for *Pinus echinata*. It would appear that even in these cases a nutritional phenomenon is involved, since the period of growth of the young pollen grains is generally correlated with the time a flower bud takes to develop which may very well be related to climate. A slow development would permit pollen grains to grow to a larger size. This hypothesis could be tested experimentally.

As this short survey demonstrates, a whole complex of different factors may have interacted to produce the often very specific and rather widely varying pollen sizes found within the angiosperms. Trends towards size increase in the fossil record may therefore be due to widely differing circumstances, although basically nutrition appears to be involved in most cases. The small size of many early Cretaceous angiosperm pollen grains is therefore most probably indicative of relatively small flowers.

#### THE WODEHOUSE EFFECT

In the foregoing chapters an attempt was made to interpret exine morphology in terms of single characters such as apertures, size, or shape, but it will be evident that this is not really possible and that to be fully understood, the exine must be studied as a whole. To redress the balance, the following chapters will attempt to discuss the exine as an integrated morphological system, by evaluating some trends which affect more than one character.

The first discussion is based on the observation by Wodehouse (1935: 393) that the absolute size of a pollen grain influences harmomegathic functioning because of the fact that in solid bodies the volume is a function of the cube of the linear dimension, while the surface area is a function of the square of the same dimension. Moreover, the shape of a solid body also influences this ratio. Hence, according to Wodehouse, the ratio between volume and surface area may become reduced in smaller as well as in more elongated grains to such degree that exine elasticity by itself can accommodate the necessary changes in volume without the need for elaborate colpate harmomegathic structures. A larger grain would, in contrast, need a larger amount of harmomegathic space to accommodate a comparable volume reduction.

This effect, which is here termed the "Wodehouse effect" in honor of its discoverer, may very well have caused pollen-morphological trends in which size, shape, and apertures coevolved.

Wodehouse actually described its operation in connection with his detailed interpretation of the pollen types in *Polygonum*, but the same principle applies to other pollen types as well.

In general terms and starting from the sphere as the basic pollen shape, it

states that any increase in size needs a larger reduction in diameter to accommodate a given percent of volume reduction and hence more elaborate harmomegathic structures to accommodate the larger stresses.

Furthermore, for the same volume a change from a sphere to a more cylindrical, prolate shape needs a smaller reduction in diameter to achieve a given percent of volume reduction and therefore less elaborate harmomegathic structures to accommodate the smaller stresses. Thus the tricolpate harmomegathic system is better adapted to the prolate than to the spherical shape.

For the change from a sphere to a disclike, oblate shape, the same reasoning applies, except that colpate harmomegathic structures are, as already mentioned earlier, structurally less well adapted to this shape and are, in fact, often replaced by pores and other harmomegathic devices.

However, the Wodehouse effect may to a certain degree be counterbalanced by the relation existing between evaporation rate and volume, the smaller spherical grains evaporating relatively more rapidly than the larger grains and the prolate and oblate ones more rapidly than the spherical ones for the same volume. It obviously depends on the sealing properties of the exine how far this second principle counteracts the Wodehouse effect. In a case like *Dipterocarpoideae*, where the harmomegathic structures of the larger grains are strikingly similar to those of the smaller ones, it would seem that the Wodehouse effect has not resulted in any change in these structures because of this counterbalancing effect, the larger grains being less liable to suffer damaging water losses. In a case like *Polygonum*, as described by Wodehouse, efficient lipid sealing may have decreased the difference caused by the ratio volume/evaporation rate to such an extent that the Wodehouse effect has been a dominant factor in the evolution of the various pollen types. Of course, to demonstrate these interactions would involve precise measurements of transpiration rates, elasticity of the exine, and presence of sealing layers, and Payne (1972) has made a first attempt in this direction. The present discussion is therefore mainly intended to draw the attention of pollen morphologists to the theoretical possibility that these physical constraints may in certain cases have guided the integrated evolution of size, shape, and harmomegathic structures.

#### BREVIAXY

Van Campo (1966, 1976) has discussed in detail this widespread tendency for a spherical grain to develop towards a disc-shaped oblate type, caused by a relative shortening of the polar axis. If this spherical grain would be tricolpate and there would be no change in aperture condition, this would result in a considerable change in the distribution of harmomegathic stresses, as already mentioned earlier. Equatorial infolding of the colpi becomes more difficult and changes in volume will be more easily absorbed by overall changes in shape by shortening or lengthening of the polar axis, the equatorial belt acting as a hinge zone. This transference of function is probably the basic cause of the commonly observed reduction of ectoapertures. In other cases the ectoapertures become thin and superficial and tend to fuse at the poles (syncolpate condition) which permits only a limited amount of infolding, with stresses more equally distributed

over the polar hemispheres. In both cases a change from a circular towards a triangular outline accompanies the apertural changes. In case of concomitant reduction of ectoapertures the apertural corners tend to become rigid, while volume reduction mainly takes place both by shortening of the polar axis and by invagination of the mesocolpia.

In the case of *Tilia* pollen, although typically brevix, this process is not as yet far advanced. The circular equatorial outline shows infolding around the very much reduced ectoapertures. The pronounced collarlike strengthening of the endoapertures may prevent rupture when infolding is too strong. The exine architecture is uniform.

In *Plagioscyphus* (Sapindaceae, Fig. 6) the interapertural outline becomes concave in the shrunken condition, and the annulate endoapertures have become rigid areas, while the harmomegathic movements have been mainly restricted to the interapertural areas where exine differentiation has taken place. Clearly, compared to *Tilia* a more specialized system of harmomegathic functioning has evolved.

The architecture of *Bombax* pollen is again different. Here the ectoapertures have shortened but are not reduced as in the preceding types and have an interangular position. They are surrounded by a heavy reticulate exine pattern, clearly reinforcing the apertures and preventing infolding. In contrast, the interapertural areas have a thin flexible exine which accommodates harmomegathic movements.

Within the brevix trend these three pollen types thus represent different ways of harmomegathic functioning, in which shape, apertures, and exine architecture are closely integrated.

#### LONGIAXY

In the longiax modification of the basic spherical shape the polar axis is elongated relative to the equatorial diameter, leading generally to more or less spindle-shaped prolate grains. The very widespread occurrence of this type as well as its early origin are probably due to the fact, mentioned before, that the tricolpate apertural system is best adapted to the longiax shape. Nevertheless, secondary modifications in shape, apertures, and exine structure do occur.

One interesting shape modification is the equatorial constriction leading to a dumbbell-shaped grain. This is well known from Umbelliferae (Cerceau-Larrival, 1967), but it occurs also, more rarely, in other unrelated families. One such case is the genus *Diplopeltis* (Sapindaceae) in which it only occurs in *D. huegelii*, the other species having developed a different shape and exine structure (Fig. 7). Basically this type represents a transfer of harmomegathic functioning from the colpi to the equatorial belt where exine thickness also has become reduced. In *D. huegelii* ectoapertures are not reduced, in contrast to most dumbbell-shaped umbelliferous pollen grains.

Very different modifications of the longiax shape are present in the fossil genus *Aquilapollenites*, in which a long polar axis is combined with protruding pores and reduced colpi. Here, the meridionally oriented harmomegathic areas appear to have been shifted to an intercolpate position, the pores acting, as in some brevix types, as rigid areas.

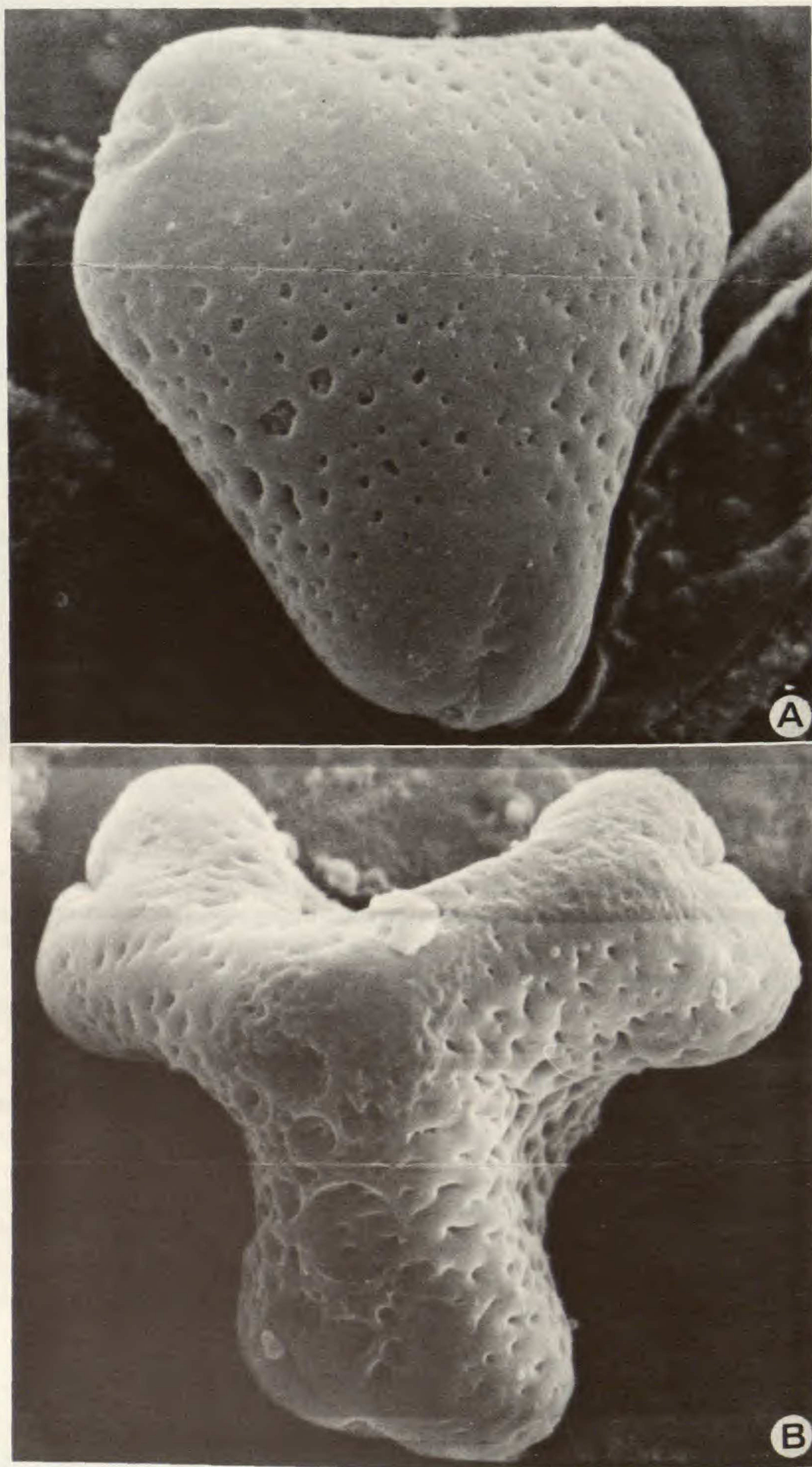


FIGURE 6. *Plagioscyphus nudicalyx* (Sapindaceae).—A. Expanded grain showing the triangular shape and rounded apertural corners with short, narrow colpi and the relatively large and scattered lumina on the equatorial part of the mesocolpia, decreasing in size towards poles and apertures. SEM.



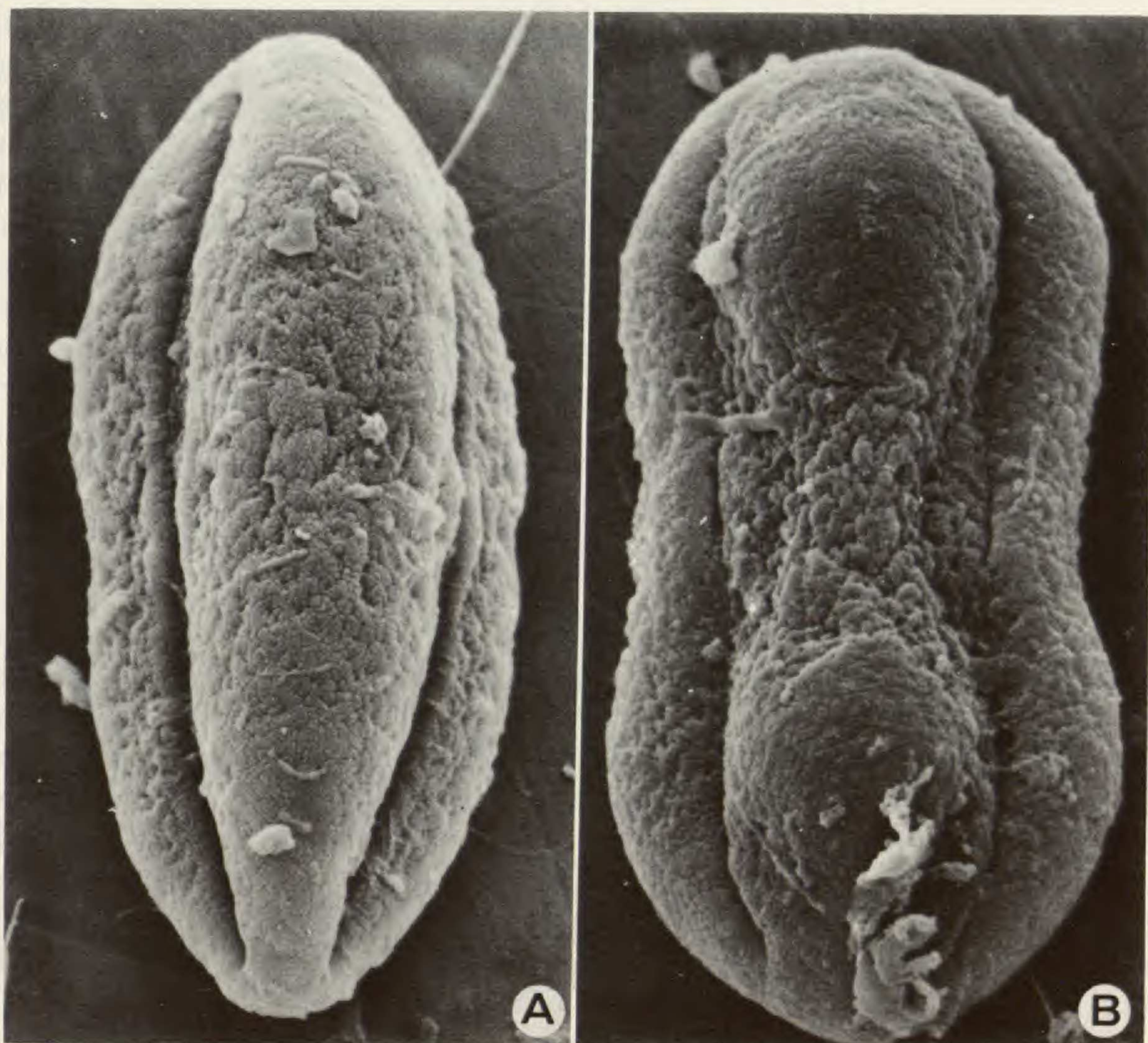


FIGURE 7. *Diplopeltis* (Sapindaceae).—A. *D. eriocarpa*. Spindle-shaped pollen grain showing long, distinctly invaginated colpi without any exterior differentiation at the site of the endoapertures and with a slightly coarser exine structure on mesocolpia. SEM, acetolyzed, 2,500 $\times$ .—B. *D. huegelii*. Dumbbell-shaped pollen grain with rather rigid polar areas due to thickened exine and more flexible equatorial belt with a loosely structured exine. The fairly long colpi show only a moderate amount of invagination. SEM, acetolyzed, 3,300 $\times$ .

#### TRENDS IN TECTUM PATTERNS

The question whether the architecture of the tectum has any special functional significance has already been reviewed in general terms before. In this chapter its relation to the possible harmomegathic functioning of the entire exine will be discussed.

The earliest Cretaceous tricolpates, dating from the Aptian (zone C-VII of Doyle et al., 1977), are characterized by a uniform reticulate tectum, and this type still persists in families such as Menispermaceae, Dilleniaceae, and Flacourtiaceae. However, only slightly later in the Aptian (zone C-IX of Doyle et

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acetolyzed, 3,100 $\times$ .—B. Contracted grain, showing invaginated mesocolpia with partly closed lumina while apertural areas have remained rigid due to endexinous thickenings. The short colpi are hardly invaginated. SEM, acetolyzed, 4,300 $\times$ .

al., 1977) a differentiation starts between more coarsely reticulate mesocolpia and finer reticulation alongside the colpi. A similar differentiation takes place simultaneously in the reticulate monocolpate pollen group leading to the first recognizable monocotyledonous pollen types (Doyle, 1973). Since these changes generally involve also a differentiation in exine thickness, the more coarsely reticulate zones having a thicker exine, it would appear that this could be interpreted as an increase in harmomegathic efficiency. The primary folding function of the aperture membranes are thus extended to the bordering tectal zones which gradually change from thin, flexible marginal areas to the more rigid central mesocolpia. The widespread occurrence of this pollen type in many angiosperm families testifies to its effectiveness in controlling harmomegathic movements in this way.

A second type is the striate pattern also found very early in angiosperm history (zones C-VIII and C-IX, Aptian of Doyle et al., 1977). It is widespread in families such as Anacardiaceae, Leguminosae, Sapindaceae, and Burseraceae. Here the tectum is essentially transformed into a ridged sheet, which causes folding to be forced in one direction. Characteristically this pattern remains uniform and associated with uniform exine thickness. In prolate grains the ridges tend to be meridionally oriented in harmony with the colpate direction of folding. Ridges tend to fuse in poleward direction as the mesocolpia become more narrow, but it is interesting that there is generally no equivalent symmetrical fusion at the poles, but that the ridge systems of two mesocolpia fuse, the third abutting more or less at a right angle (Fig. 8B). This situation which probably reflects ontogenetic processes, presumably under tapetal influence, causes a certain asymmetry in the stress pattern.

The difference in degree of development of the striate pattern between the two closely related subspecies of *Litchi sinensis* (Sapindaceae), shown in Fig. 8, probably reflects stages in the evolution from a basically reticulate tectum towards a finely striate one.

It appears that in breviate grains the striate pattern is less frequent. In *Talisia* (Sapindaceae) the subprolate tricolpate pollen type is striate, while the oblate one with reduced colpi has a smooth tectum (Muller & Leenhouts, 1976).

In *Allophylus* (Sapindaceae) which has oblate-triporate pollen, striate patterns occur in a minority of types, mainly in Southeast Asia, and here the ridge pattern often becomes concentric around the apertural areas as a tubular strengthening, while at the poles a more irregular, but not clearly asymmetrical pattern develops (Fig. 9).

*Allophylus cobbe* is macromorphologically highly variable which is partly correlated with ecology (Leenhouts, 1967), but the pollen-morphological variation in tectum pattern shown in Fig. 10 is not correlated and appears to have evolved

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FIGURE 8. *Litchi sinensis* (Sapindaceae).—A. Subsp. *javensis*. Oblique equatorial view showing meridional orientation of striae at the margins of the colpi, while on the mesocolpia a more irregular orientation is present. The small isodiametric lumina visible between the ridges indicate that the ridges have probably developed over a finely reticulate tectum. SEM, acetolyzed, 5,000 $\times$ .—B. Subsp. *philippinensis*. Polar view showing a dense, finely striate pattern, meridionally oriented but with asymmetric fusion of ridges at the pole. SEM, acetolyzed, 5,000 $\times$ .



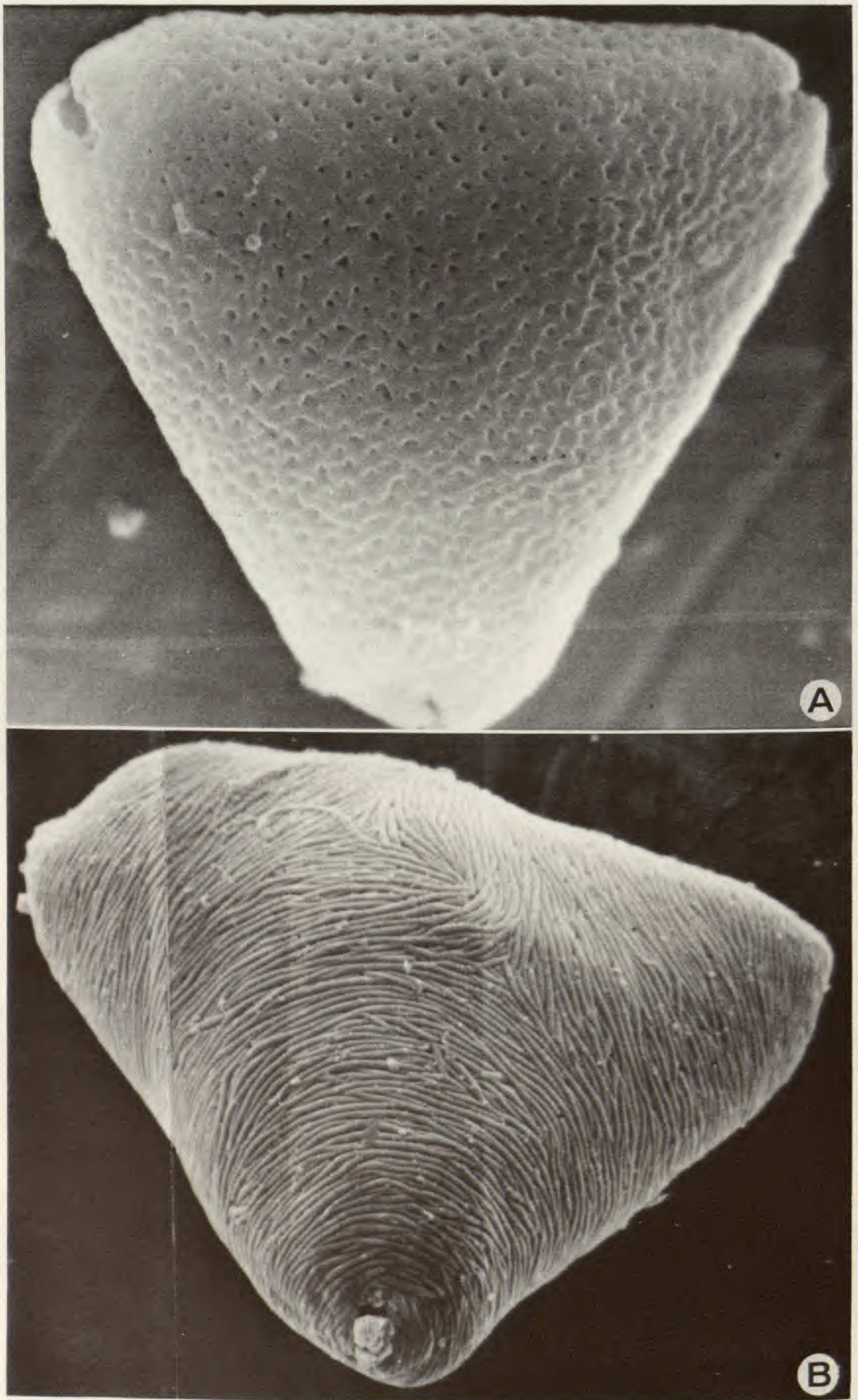


FIGURE 9. *Allophylus cobbe* (Sapindaceae).—A. Uniformly finely reticulate pollen type in polar view, small, irregularly porate-colpate apertures. *Dequaire 27678*, Madagascar. SEM, acetolyzed, 4,300 $\times$ .—B. Finely striate pollen type in oblique polar view showing porate apertures with concentrically arranged striate pattern. Slightly irregular fusion of ridges at poles. *Kostermans 807*, Thailand. SEM, acetolyzed, 3,700 $\times$ .

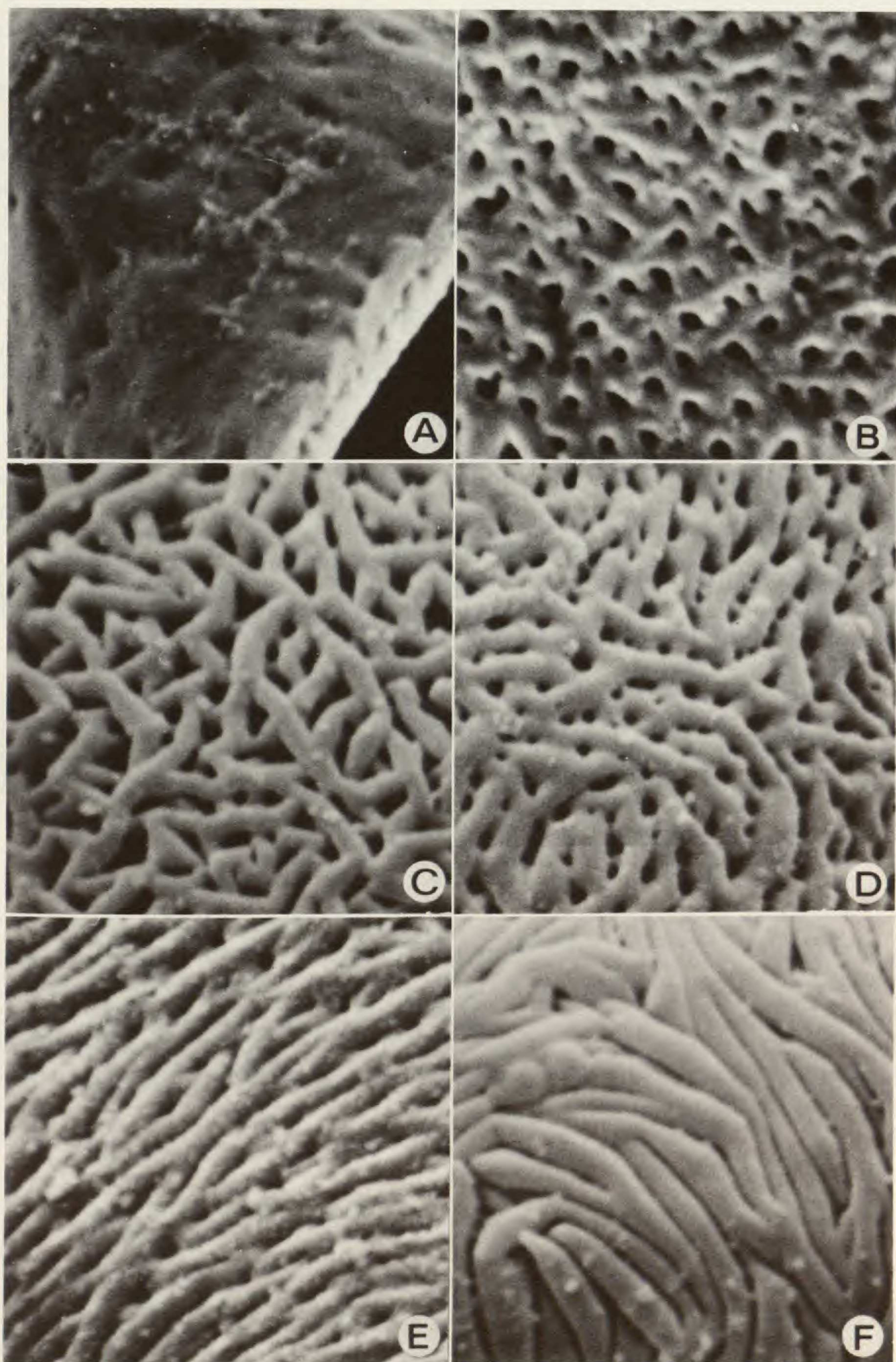


FIGURE 10. *Allophylus cobbe* (Sapindaceae), tectum patterns.—A. Nearly smooth, with scattered perforations. Section of exine shows sole, very short columellae and tectum. Rare, restricted to Sumatra and Borneo. *Korthals* s.n., Sumatra.—B. Finely reticulate. Restricted to Madagascar, New Guinea, and Pacific islands. *LB 12002*, Madagascar.—C. Retirugate. Restricted to South America. *Hassler 12231*, Paraguay.—D. Striate-reticulate. Dominant type occurring in all areas. *King 351*, Andamans.—E. Finely striate. Restricted to Southeast Asia. *Rabil 42*, Thailand.—F. Coarsely striate. Very rare, only found in Viet Nam. *d'Alleizette 1919*, Viet Nam. SEM, acetolyzed, 10,000 $\times$ .

quite independently. The different patterns are difficult to understand other than as different structural solutions to stress absorption.

The functional significance of a third basic tectal structure, the Crotonoid pattern, which is also known to emerge very early in the fossil record (*Stellatopollis*, probably Barremian, cf. Doyle et al., 1977) is more difficult to interpret, although it may be considered a system of excrescences which upon volume reduction achieves efficient closure around porelike structures. Its apparently independent evolution in unrelated angiosperms suggests at least some adaptive advantage. It is remarkable, however, that the pseudocrystalline aspect of this structure is matched in the rigid wall patterns of certain tripylean Radiolaria.

A closed, smooth-surfaced tectum appears to be in many cases a secondary modification, especially in wind-pollinated species. However, in *Lepisanthes* (Sapindaceae), the breviate pollen type of *L. tetraphylla schizolepis* has evolved a very thin, flexible psilate exine over the harmomegathic areas, in contrast to the related *L. fruticosa* in which the reticulate ectexine is considerably thickened on the mesocolpia, accentuating the meridional folding of the colpi. Both species are insect pollinated (Muller & Leenhouts, 1976).

In the cases discussed here the tectal architecture is clearly integrated with aperture type and shape into a structure which allows maximum harmomegathic movement with a minimal chance of rupture of the exine.

#### PERISTASY

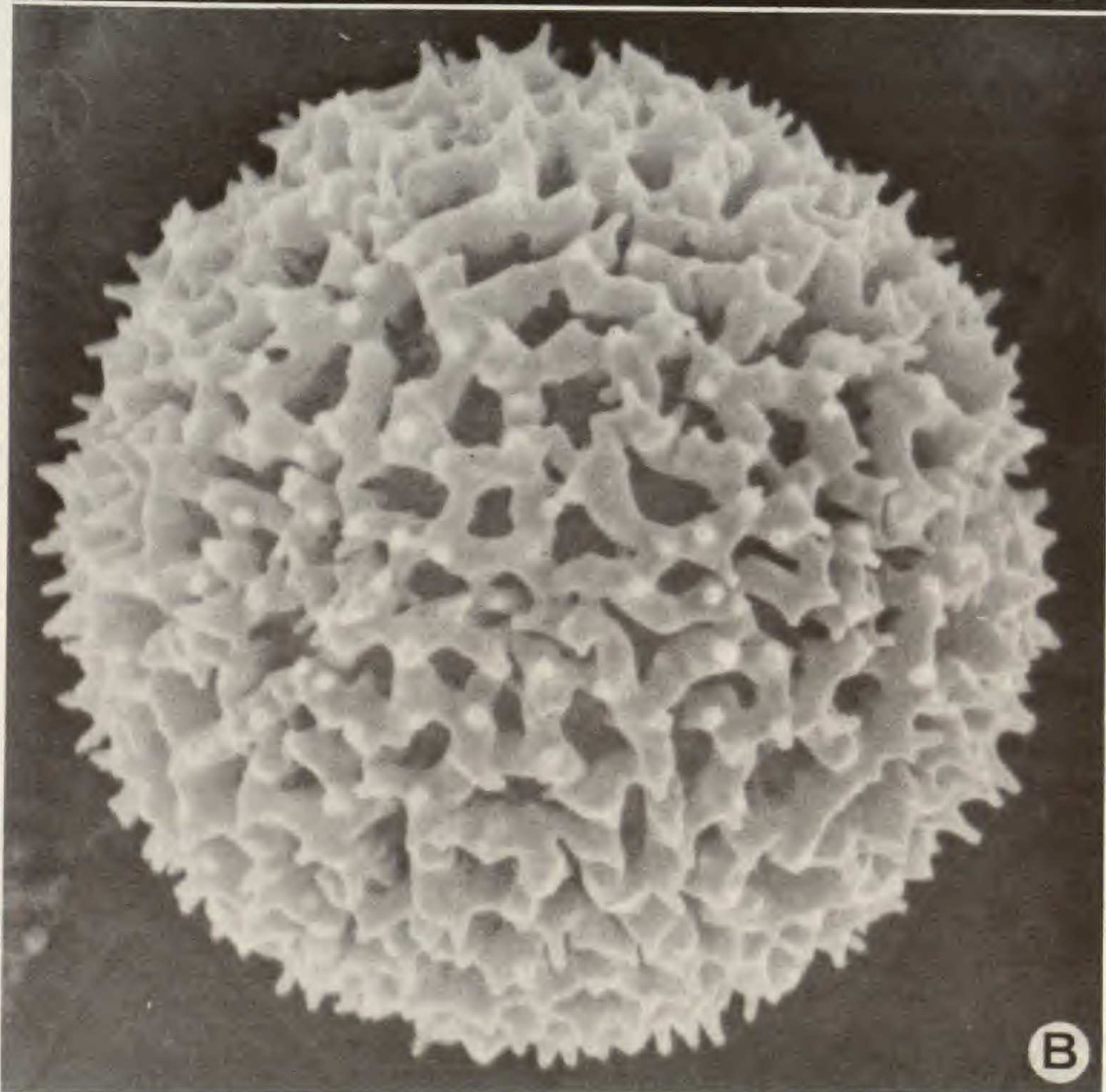
The term peristasy refers to a trend which develops from the basic tricolporate pollen type by reduction of ectoapertures and concomitant changes in exine structure towards a uniform distribution of harmomegathic forces over a sphere (from the Greek: peri = all around; stasis = rigidity).

Although structurally the peristatic type resembles the peri-aperturate end product of the successiform series, it differs strikingly in the ectoapertural reduction, and it could perhaps best be described as a disruption of the trend towards combination of ecto- and endoapertural functions in one structure. The disappearance of the meridionally oriented colpate folding structures is accompanied by the development of a more uniform reticulate pattern. The ectexine thickness and coarseness of the reticulum generally increases also. The endoapertures may persist underneath the reticulate ectexine, and the grains are then called cryptoporate. This trend is demonstrated for the genus *Harpullia* (Sapindaceae) in Fig. 11. A similar trend is apparent in Flacourtiaceae (*Hydnocarpus*, Schaeffer, 1972), Icacinaceae (*Gonocaryum*, Lobreau-Callen, 1972), Bignoni-

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FIGURE 11. *Harpullia* (Sapindaceae).—A. *H. alata*. Equatorial view showing the relatively short, colpate ectoaperture, closed by a membrane which is covered with small spinules, without any clear indication of the endoapertures situated underneath. Tectum rather finely reticulate-echinate, slightly finer along colpus margins. NSW 136084, Australia. SEM, acetolyzed, 4,400 $\times$ .—B. *H. crustacea*. Acolpate, endoapertures entirely hidden (cryptoporate). Tectum uniformly coarsely reticulate with broad ridges and heavy columellae, thus able to distribute harmomegathic stresses equally over the surface of this perfectly spherical grain (peristasy). NGF 11839, New Guinea. SEM, acetolyzed, 5,100 $\times$ .



aceae (*Pithecoctenium*, Buurman, 1977), Dichapetalaceae (*Dichapetalum timoriense*, Punt, 1975), and Loganiaceae (*Fagraea*, Punt, 1978).

For Compositae, Wodehouse (1935) had already drawn attention to the demobilization of furrows and the transfer of the harmomegathic function to the enlarged pores in the lophate liguliferae-pollen type. Basically this is also a peristatic structure, in which the heavy cristae distribute stresses equally over the spherical surface providing an outer rigid structure, comparable to a geodesic dome. Within this structure, as recently discussed by Bolick (1978), the inner endexinous hull and the porate apertures are free to expand or contract according to the state of desiccation of the protoplasm.

Also the pollen grains of *Persicaria* can be considered peristatic. As Wodehouse (1935: 392) already pointed out, the elaborate reticulate system of high ridges imparts a stiffness to the exine, and furrows have disappeared. However, in this case pores have become more numerous, and on this aspect the pollen type might also be assigned to the successiform series.

#### FLEXIBLE EXINES

In contrast to the trend towards a stiffened exine, a trend towards extreme flexibility of the exine can be distinguished. Wodehouse (1935: 392) already recognized this basic structural design in anemophilous members of Polygonaceae (*Rumex*, *Rheum*, *Muehlenbeckia*), in which the colpi are reduced to long linear grooves with negligible width, even when expanded, and which have retained small endoapertures. The exine is relatively thin and finely and uniformly reticulately structured, while the shape is approximately spherical. When drying out, the colpi act as hinges and the thin, flexible exine follows the shape of the shrinking protoplast. An essentially similar structural principle characterizes certain Dipterocarpaceae (*Dryobalanops*, *Dipterocarpus*, cf. Maury et al., 1975). As shown in Fig. 4G, here also the colpi are long and narrow, and the exine is thin, without endexine and uniformly structured. However, the ectexine is not reticulate but, as pointed out before, has evolved into a peculiar urn-shaped tilioid pattern in which tectum and columellae are fused into a structural design which permits bending in all directions. This flexibility is, moreover, enhanced by the absence of the endexine and the reduction of the sole to a thin, lamellated basal layer. Also, in *Rumex acetosella* pollen a similar reduction to a basal, lamellar layer appears to have taken place (Nilsson et al., 1977).

For Polygonaceae, Wodehouse (1935) supposed this pollen type to have evolved in relation to anemophily, but in the dipterocarp genera mentioned, which are insect pollinated, this is unlikely. It appears more probable that in both cases the development of this specialized pollen type reflects a unique solution to harmomegathic stress accommodation.

This case demonstrates how in taxonomically distant families functionally similar pollen types have evolved, with a similar aperture structure and a reduced, but in detail significantly different exine architecture.

#### LATISTASY

This term is introduced for pollen types in which the harmomegathic stress distribution pattern is latitudinally oriented. The most typical examples are the equatorial costae bordering the encircling endopertures in certain species of



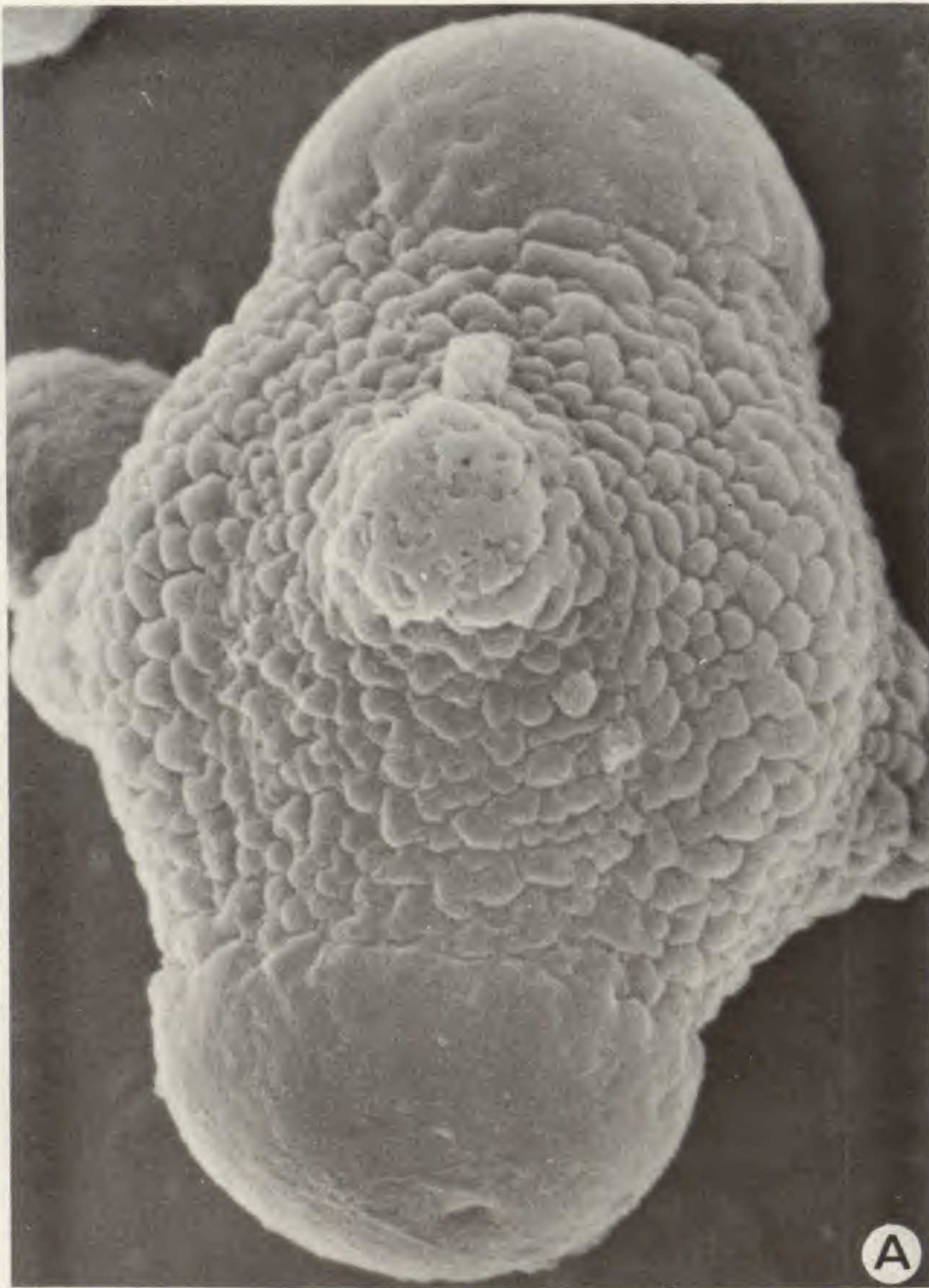


FIGURE 12. *Xanthophyllum bullatum* (Polygalaceae). Oblique polar view showing the relatively smooth-surfaced polar cap, the short colpi with characteristically rounded tips and widening at the equator but without any possibility for invagination due to endexinous costae bordering the broad, equatorial-encircling endoaperture. The mesocolpia are thin over the endoaperture, effectively separating the pollen grain in two rigid halves, connected by flexible strips of exine which act as the main latitudinally oriented harmomegathic structures (latistasy). SEM, acetolyzed, 4,000 $\times$ .

*Utricularia* (Lentibulariaceae), *Xanthophyllum* (Polygalaceae), and *Rhizophora* (Rhizophoraceae, Muller & Caratini, 1977).

In the case of *Xanthophyllum* (Fig. 12) the colpi do not act as folding structures and the volume accommodation appears to have been entirely transferred to the flexible strips of mesocolpia connecting the rigid polar areas.

In *Rhizophora* the three colpi may be more or less distinctly developed, according to the species, but they appear not to act as folding structures. In *R. racemosa* they are most strongly reduced, while the shape has become suboblate, and the polar area appears to be more flexible in comparison to the spherical grains of *R. mucronata* which have a thickened polar exine with a microreticulate



structural differentiation. Thus *R. racemosa* pollen appears to be more advanced in the trend towards latistasy than the pollen of the other species of the genus.

In the pollen grains of *Sonneratia caseolaris* a latistatic structure is apparent, as shown by the latitudinal hinge line separating the rigid, smooth, and thick polar cap from the more flexible verrucate equatorial belt (Muller, 1978). It is of interest that an essentially similar pollen type has been described by Nowicke & Skvarla (1974) in *Tournefortia*, pollen type II. The two pollen types are compared in Fig. 13 and show a remarkable correspondence in shape and sculptural distribution but differ in the presence of reduced ectocolpi in *Tournefortia*. In ultrastructure there is also correspondence in the thick endexine over the equatorial belt which rather abruptly becomes very thin over the polar area, but the structure of the ectexine at the poles again differs slightly. Nowicke & Skvarla (1974) could find no relation between pollen types and environment or pollination vector in *Tournefortia*, while also in *Sonneratia* the different pollen types can not be related to environmental factors. The convergent development of a highly specialized, functionally comparable pollen structure in such taxonomically widely separated genera is therefore an indication that factors relating to harmomegathic efficiency may have been at work.

#### CONCLUSIONS

The preceding discussion shows, for a few selected examples, how far exine morphology can be understood as a result of different processes. Primary are the limitations imposed by the physicochemical process of sporopollenin deposition, the induction of apertures, and growth processes. These are the nomothetical aspects of form development referred to by Van Campo (1976). Next are the inherited structures such as colpi which may be changed or eliminated in the evolutionary process if their function changes or is transferred. Finally there is the innovative aspect leading to new structures such as endoapertures, spines, and novel harmomegathic systems.

In general pollen morphology follows the principle of evolutionary canalization (Stebbins, 1975). This is based on conservation of organization, causing preservation of structures already evolved and only slow modification without inadapative intermediate stages and adaptive modification along the lines of least resistance. These changes are more likely to occur because they are based on the smallest possible number of gene substitutions.

This explains why, once a certain adaptive level such as peristasy, the heterocolpate condition, brevixy with syncolpy, or the triporate condition has been reached, further development is more likely to lead to further refinements than to radically new types. In Lecythidaceae, for instance, once the syncolpate type

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FIGURE 13.—A. *Sonneratia caseolaris* (Sonneratiaceae). Equatorial view showing protruding pores covered with irregularly verrucate exine, absence of ectoapertures, densely verrucate equatorial belt and smooth polar caps. SEM, acetolyzed, 2,470 $\times$ .—B. *Tournefortia hispida* (Boraginaceae). Equatorial view showing protruding pores covered with large verrucae, separated by narrow colpate ectoapertures which can invaginate only in a limited way, densely verrucate equatorial belt and smooth polar caps. SEM, acetolyzed, 3,750 $\times$ . Courtesy Dr. J. Nowicke.

originated, further development appears to have been canalized into refinements in aperture construction (Muller, 1973).

To this, the principle of transference of function, as stated by Corner (1958), should be added. It appears to have been operative in some of the cases of harmomegathic adaptations cited in this paper.

Although many aspects of exine morphology, especially those connected with the reservoir function, still defy analysis, it has nevertheless become clear that the pollen wall represents a highly complex system in which many different and often temporally spaced functions are closely integrated. The large variability of angiosperm exine morphology probably reflects compromises between the different functional aspects, often with one function dominating. This will depend primarily on the ecological situation but will then often lead to evolutionary canalization of structural development.

This interpretation is of importance when exine characters are utilized in taxonomy. Structural features should be evaluated within the general adaptive context, and this is especially important in numerical approaches to palynotaxonomy (Hideux, 1977), which run the risk of overestimating the number of truly independent exine characters.

Also, the recognition of separate morphological trends as a base for taxonomic evaluation (Punt, 1976) should be complemented by a consideration of functional interdependence. This is especially important for recognition of the many striking convergences which are so widespread in angiosperm pollen types.

Finally, the interpretation of the fossil pollen record can be considerably broadened if the structures preserved are interpreted in terms of function and ecological significance for the plant as a whole. Doyle (1977) has recently made a first attempt in this direction in his analysis of the morphological evolution of early Cretaceous angiosperm pollen types.

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